Université du Québec à Rimouski

Dynamique des populations de tortues marines en ponte sur trois plages de la Martinique

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« There are some four million different kinds of animals and plants in the world. Four million different solutions to the problems of staying alive. »

Sir David Attenborough

« As a naturalist you will never suffer from that awful modern disease called boredom — so go out and greet the natural world with curiosity and delight, and enjoy it. »

Gerald Malcolm Durrell

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RÉSUMÉ

Les tortues marines sont des espèces emblématiques de nos océans et sont toutes classées sur la liste rouge de l'UICN. La Martinique, une île des Petites Antilles dans le sud de la Caraïbe, est un site de ponte prisé des tortues luth (*Dermochelys coriacea*) et des tortues imbriquées (*Eretmochelys imbricata*). Selon l'UICN, la tortue luth a connu un déclin d'au moins 80 % au cours des trois dernières génération, et la tortue imbriquée a vu ses populations chuter d'environ 90 % à l'échelle mondiale au cours du dernier siècle. Des diminutions importantes qui poussent à mieux comprendre ces espèces afin d'adapter les mesures de conservation. Ce mémoire se concentre sur les populations de tortues luth et imbriquées de trois sites de ponte majeures de la Martinique.

Le premier objectif de ce mémoire consiste à évaluer l'impact d'un ouragan précoce sur la saison de ponte de nos deux espèces de tortues marines, phénomène appelé à s'intensifier avec les changements globaux actuels. L'étude a couplé des observations terrain, des cartographies des emplacements des nids, ainsi que du suivi de la ligne d'eau, avant, pendant et après l'ouragan. Les résultats ont montré une plus grande vulnérabilité des tortues luth face à ces évènements climatiques extrêmes, expliquée par une période de nidification plus courte et plus tôt ainsi que des emplacements de nids plus proches de l'eau que pour la tortue imbriquée.

Le second objectif portait sur une évaluation de traits comportementaux des femelles en ponte à l'aide de la photo-identification (photoID). Avec une base de données photo de 4 années de suivi, cette étude a permis d'estimer un taux de recapture des femelles et à démontrer l'intérêt de l'utilisation systématique de la photoID dans les suivis de populations. En effet, 36% des tortues imbriquées rencontrées avaient déjà été observées au cours de la même saison, ce chiffre monte à 61% pour la tortue luth. De plus, nous avons procédé à une caractérisation des micro-habitats des trois sites de ponte permettant d'évaluer les préférences spécifiques de nos tortues en termes de milieu de nidification. Enfin, nous avons mis en avant un comportement encore jamais décrit à notre connaissance, l'heure spécifique de ponte pour chaque individu de tortue imbriquée. En effet, nous avons estimé que les tortues imbriquées viennent pondre à des heures « préférentielles », à échelle de l'individu, avec un écart moyen de 1h12min ± 12 min. Ainsi, une tortue qui est sortie de l'eau à 21h, viendra deux semaines plus tard à 21h ± 1h12(±0:12min).

Enfin, le dernier chapitre de ce mémoire porte sur l'évaluation de nouveaux outils non invasifs de suivis de populations. Le premier outil porte sur l'analyse métagénomique de la composition en organismes chloroplastiques du biofilm présent sur les carapaces, à l'aide du marqueur chloroplastique 16S. Le deuxième outil s'intéresse à l'analyse de la composition en métaux des coquilles d'œufs vides analysé par spectrométrie de masse à plasma à couplage inductif (ICPMS). Nos résultats montrent que ces outils permettent d'observer de fortes différences interspécifiques, notamment la composition du biofilm qui est très diversifiée chez la tortue imbriquée et quasi nulle chez la tortue luth. La composition en métaux des coquilles d'œufs reflète bien les différences de niveau trophique de nos espèces de tortues étudiées, avec des tortues luth plus contaminées lié à leur plus forte capacité à bio-amplifier. Enfin, ce chapitre a également mis de l'avant les lacunes dans des bases de données de référence taxonomique, avec seulement 16% des OTUs (Unité Taxonomique Opérationnelle) identifiées au niveau de l'espèce.

L'ensemble de ces résultats permettent de dessiner un meilleur portrait des tortues luth et imbriquées de Martinique. Ils permettent d'apporter de nouvelles connaissances scientifiques et des indicateurs alternatifs pour l'étude de l'écologie et la conservation des tortues marines, afin d'aider aux futures prises de décision en matière de conservation.

Mots clés : Tortues marines, *Dermochelys coriacea*, *Eretmochelys imbricata*, Martinique, Conservation, Changement climatique, Photo-identification, Biofilm, Métaux traces.

ABSTRACT

Sea turtles are iconic species of our oceans and are all listed on the IUCN Red List. Martinique, an island in the Lesser Antilles in the southern Caribbean, is a prized nesting site for leatherback (*Dermochelys coriacea*) and hawksbill (*Eretmochelys imbricata*) turtles. According to the IUCN, the leatherback turtle population has declined by at least 80% over the last three generations, and the hawksbill turtle population has decreased by approximately 90% globally over the last century. These significant declines underscore the need for a better understanding of these species to adapt conservation measures. This thesis focuses on the leatherback and hawksbill turtle populations of three major nesting sites in Martinique.

The first objective of this thesis was to assess the impact of an early hurricane on the nesting season of our two sea turtle species, a phenomenon expected to intensify with current global changes. The study combined field observations, such as mapping nest locations and monitoring the waterline, before, during, and after the hurricane. The results showed that leatherback turtles were more vulnerable to these extreme weather events, explained by a shorter and earlier nesting period and nest locations closer to the water than those of hawksbill turtles.

The second objective focused on evaluating the behavioural traits of nesting females using photo-identification (photoID). With a four-year photo database, this study allowed us to estimate the female recapture rate and demonstrate the value of systematically using photoID in population monitoring. Indeed, 36% of the hawksbill turtles encountered had already been observed during the same season, a figure that rises to 61% for the leatherback turtle. Furthermore, we characterized the microhabitats of the three nesting sites, allowing us to assess the specific nesting environment preferences of our turtles. Finally, we highlighted a behaviour previously undescribed to our knowledge: the specific nesting time for each individual hawksbill turtle. We estimated that hawksbill turtles come ashore to lay their eggs at "preferred" times, on an individual level, with an average difference of 1 hour 12 minutes ± 12 min. This means that a turtle that emerged from the water at 9:00p.m. will return two weeks later at 9:00p.m. ± 1:12 (± 0:12).

Finally, the last chapter of this thesis focuses on the evaluation of new non-invasive population monitoring tools. The first tool focuses on the metagenomic analysis of the chloroplast organism composition of the carapace biofilm using the chloroplast marker 16S. The second tool focuses on analysing the metal composition of empty eggshells using inductively coupled plasma mass spectrometry (ICPMS). Our results show that these tools reveal significant interspecific differences, particularly in biofilm composition, which is highly diverse in hawksbill turtles and almost non-existent in leatherback turtles. The metal composition of the eggshells accurately reflects the trophic level differences among the turtle species studied, with leatherback turtles exhibiting higher contamination levels due to their greater capacity for bioamplification. Finally, this chapter also highlighted the gaps in taxonomic reference databases, with only 16% of OTUs (Operational Taxonomic Unit) identified at the species level.

Together, these results provide a clearer picture of the leatherback and hawksbill turtles of Martinique. They provide new scientific knowledge and alternative indicators for the study of ecology and conservation of sea turtles, in order to help future conservation decisions.

Keywords: Sea turtles, *Dermochelys coriacea*, *Eretmochelys imbricata*, Martinique, Conservation, Climate change, Photo-identification, Biofilm, Trace metals.

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Français, English

Al	Aluminium
ANOVA	Analyse de la Variance, Analysis of Variance
As	Arsenic
Au	Or, Gold
B	Bore, Boron
Ba	Baryum, Barium
Be	Béryllium, Beryllium
Ca	Calcium
CCL	Longueur Courbe de la Carapace, Curved Carapace Length
CCW	Largeur Courbe de la Dossière, Curved Carapace Width
Cd	Cadmium
Ce	Cérium, Cerium
CITES	Convention sur le commerce international des espèces de faune et de flore sauvages menacées d'extinction, Convention on International Trade in Endangered Species of Wild Fauna and Flora
CNRC	Conseil national de recherches Canada, National Research Council Canada

Co	Cobalt
Cr	Chrome, Chromium
Cs	Césium, Cesium
Cu	Cuivre, Copper
DEAL	Direction de l'Environnement, de l'Aménagement et du Logement
Dy	Dysprosium
ADN, DNA	Acide désoxyribonucléique, Deoxyribonucleic acid
ADNe, eDNA	ADN environnemental, Environmental DNA
EPS	Substances polymériques extracellulaires, Extracellular Polymeric Substances
Er	Erbium
Eu	Europium
Fe	Fer, Iron
Gd	Gadolinium
Ge	Germanium
GPS	Système mondial de positionnement, Global Positioning System
H_2O_2	Peroxyde d'hydrogène, Hydrogen peroxide
HAP, PAHs	Hydrocarbures aromatiques polycycliques, Polycyclic Aromatic Hydrocarbons (PAHs)
HCl	Acide chlorhydrique, Hydrochloric acid

Hf	Hafnium
HFSEs	Éléments à fort champ de force, High Field Strength Elements
Hg	Mercure, Mercury
HNO_3	Acide nitrique, Nitric acid
Ho	Holmium
ICP	Plasma à couplage inductif, Inductively Coupled Plasma
ICPMS	Spectrométrie de masse à plasma à couplage inductif, Inductively Coupled Plasma Mass Spectrometry
Ir	Iridium
La	Lanthane, Lanthanum
Li	Lithium
LILEs	Éléments lithophiles à grand rayon ionique, Large-Ion Lithophile Elements
Lu	Lutétium, Lutetium
Mg	Magnésium, Magnesium
Mn	Manganèse, Manganese
Mo	Molybdène, Molybdenum
Na	Sodium
Nb	Niobium
Nd	Néodyme, Neodymium
Ni	Nickel

ONF	Office national des forêts
OTU	Unité taxonomique opérationnelle, Operational Taxonomic Unit
P	Phosphore, Phosphorus
Pb	Plomb, Lead
PCA	Analyse en composantes principales, Principal Component Analysis
PCB	Polychlorobiphényles, Polychlorinated Biphenyls
PCR	Réaction de polymérase en chaîne, Polymerase Chain Reaction
Pd	Palladium
PERMANOVA	Analyse de la variance multivariée par permutations, Permutational Multivariate Analysis of Variance
PGEs	Éléments du groupe du platine, Platinum Group Elements
PhotoID	Photo-identification
PIT tag	Transpondeur passif intégré (micropuce), Passive Integrated Transponder tag
Pr	Praséodyme, Praseodymium
Pt	Platine, Platinum
QC	Contrôle qualité, Quality control
QGIS	SIG QGIS (système d'information géographique libre), Geographic Information System software
Re	Rhénium, Rhenium
RF matching	Accord d'impédance radiofréquence, Radio-Frequency Matching

Rh	Rhodium
RPD	Différence relative en pourcentage, Relative Percent Difference
rRNA	ARN ribosomique, Ribosomal RNA
RSD	Écart-type relatif, Relative Standard Deviation
Ru	Ruthénium, Ruthenium
Sb	Antimoine, Antimony
Sc	Scandium, Scandium
SD	Écart-type, Standard Deviation
Se	Sélénium, Selenium
Sm	Samarium, Samarium
Sn	Étain, Tin
Sr	Strontium
Ta	Tantale, Tantalum
Tb	Terbium
Te	Tellure, Tellurium
Th	Thorium
Ti	Titane, Titanium
Tl	Thallium
Tm	Thulium
ETM, TMEs	Éléments traces métalliques, Trace Metal Elements

U	Uranium
IUCN, UICN	Union internationale pour la conservation de la nature, International Union for Conservation of Nature
V	Vanadium
Y	Yttrium
Yb	Ytterbium
Zn	Zinc
Zr	Zirconium

INTRODUCTION GÉNÉRALE

1. LES TORTUES MARINES

1.1 Généralités

Les tortues marines sont des espèces jouant un rôle clé dans l'équilibre des écosystèmes marins (Bouchard & Bjorndal, 2000; Bjorndal et al., 2003; Hannan et al., 2007). Ces reptiles, appartenant à l'Ordre des Testudines et à la Super-Famille des Chelonioidea, sont étroitement liés aux écosystèmes océaniques, mais également terrestres, dont ils dépendent pour leur nidification (Hannan et al., 2007). Il existe de nos jours sept espèces de tortues marines classées en deux familles principales : les Dermochelyidae et les Cheloniidae (**Fig. 1**; Lutz & Musick, 1997; Lescure, 2001). Cette dernière se caractérise par des individus à carapaces dures à écailles et inclut six espèces (Lutz & Musick, 1997) - la tortue Verte (*Chelonia mydas*; Linnaeus, 1758), la tortue Caouanne (*Caretta caretta*; Linnaeus, 1758), la tortue imbriquée (*Eretmochelys imbricata*; Linnaeus, 1766), la tortue Olivâtre ou tortue de Ridley (*Lepidochelys olivacea*; Eschscholtz, 1829), la tortue de Kemp (*Lepidochelys kempii*; Garman, 1880) et la tortue à dos plat (*Natator depressus*; Garman, 1880). Les Dermochelyidae, dont la seule représentante est la tortue luth (*Dermochelys coriacea*; Vandelli, 1761), sont caractérisées par une carapace en peau dénuée d'écailles (Lutz & Musick, 1997; Lescure, 2001).

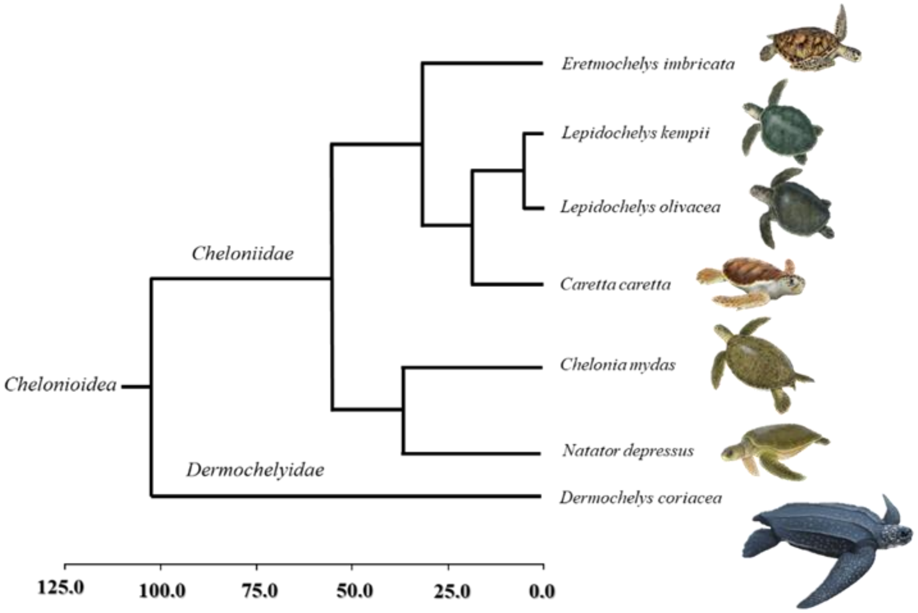

Figure 1. Relation phylogénétique des Chelonioidea (selon l’hypothèse de Thomson et Shaffer, 2010; Illustrations de ©NOAA Fisheries).

On estime que les tortues marines modernes ont commencé à sillonner les océans il y a 110 à 120 millions d’années (Crétacé inférieur), adaptant leur physiologie et leurs comportements à des environnements variés, allant des eaux tropicales chaudes aux régions tempérées et froides (Zangerl, 1980; Eckert et al., 1989; Hays et al., 2004). En effet, toutes les espèces de tortues marines migrent à un rythme saisonnier entre leurs aires de reproduction (tropicales ou intertropicales) et leurs aires d’alimentation, et ce, sur de longues distances (Sternberg, 1981; Dodd, 1988). Elles peuvent parcourir jusqu’à 18 000 km par an, en particulier la tortue luth, qui migre entre des zones tropicales et des eaux tempérées plus froides, comme le golfe du Saint-Laurent, pour se nourrir (Ferraroli et al., 2004; James et al., 2005a ; James et al., 2007; Hays et al., 2006; Davenport et al., 2014). Les tortues marines jouent également un rôle clé dans les écosystèmes côtiers en transférant des nutriments marins vers les plages et les forêts littorales via leurs œufs. Les œufs non éclos enrichissent le sol en azote et phosphore, favorisant la croissance de la végétation qui stabilise les dunes et prévient l’érosion (Bouchard & Bjorndal, 2000; Hannan et al., 2007). Cette fonction écologique essentielle relie directement les écosystèmes marins et terrestres (Madden et al., 2008).

Cycle de Vie

Les tortues marines sont des espèces longévives à maturité tardive (Lutz & Musick, 1997; Scott, Marsh & Hays, 2012). L’espérance de vie varie en fonction de l’espèce, mais en moyenne elles atteignent 62 ans, et jusqu’à 90,4 ± 5,3 ans pour la tortue luth (Mayne et al., 2020). Les sept espèces de tortues marines possèdent un cycle de vie similaire (**Fig. 2**), avec des pontes en milieu tropical (Hendrickson, 1980; Hirth, 1980; Van Buskirk & Crowder, 1994). Les tortillons (bébés tortues) éclosent après environ 60 jours selon les conditions d’incubation, telles que la température et l’humidité du sol (Chevalier & Lartiges, 2001; Lescure, 2001; Maulany et al., 2012; Rafferty et al., 2017). La température joue un rôle important dans la détermination du sexe des tortillons, avec un seuil à 29,5 °C pour une production de femelles. Sous cette température, les tortillons seront des mâles (Janzen, 1994). Ainsi, les œufs plus proches de la surface sont majoritairement des femelles et ceux plus au fond de la cavité, des mâles, ce qui permet un certain équilibre (Lutz & Musick, 1997).

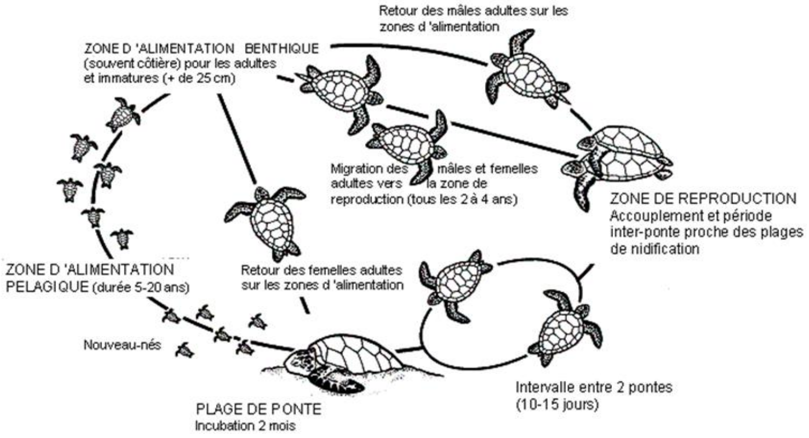

Figure 2. Cycle de vie schématisé des tortues marines (modifié, d’après Lanyon et al., 1989 et FAO, 2009).

Une fois sortis de leur nid creusé dans le sable, les tortillons se dirigent vers le point le plus lumineux, soit la mer (Lorne & Salmon, 2007). Débute alors la phase dite « des années perdues », qui dure entre 1 et 10 ans et qui est peu documentée (Phillips et al., 2025). Il est généralement admis que les tortillons, dérivent passivement en se nourrissant dans le milieu pélagique (Carr, 1987; Musick & Limpus, 1997; Hays et al., 2010; Scott et al., 2014). Toutefois, les données récentes obtenues grâce aux balises GPS suggèrent qu'ils nagent activement vers des habitats de surface, notamment les amas d'algues du genre *Sargassum* sp., qui leur offrent à la fois des ressources alimentaires et une protection contre les prédateurs (Putman & Mansfield, 2015; Phillips et al., 2025). Hormis la tortue luth, espèce au mode de vie majoritairement pélagique, plusieurs autres espèces (e.g. verte, imbriquée, Ridley, et de Kemp) débutent leur phase d'alimentation côtière autour de 20–30 cm de longueur de carapace, dans l'Atlantique Ouest (Bjorndal & Bolten, 1988). La caouanne, elle, effectue généralement ce basculement autour de 46–64 cm (Bjorndal et al., 2000). Il existe une exception à cette phase pélagique, la tortue à dos plat (*Natator depressus*) qui n'effectue pas de dispersion océanique et qui reste dans les eaux côtières qui l'ont vue naitre (Walker & Parmenter, 1990). Cela expliquerait son endémisme du nord de l'Australie (Walker & Parmenter, 1990). Chez toutes les espèces de tortues, le stade de subadulte débute lors de l'apparition des caractères sexuels secondaires, notamment chez les mâles, tels que l'allongement de la queue et des griffes antérieures (Taquet, 2007). Finalement, le stade reproducteur adulte débute entre 15 et 30 ans en fonction de l'espèce (Avens & Snover, 2013). La reproduction chez toutes espèces confondues implique une migration vers des zones spécifiques où se rejoignent mâles et femelles d'une même population (Chevalier & Lartiges, 2001). Limpus et al. (1992) soulignent que ce comportement va à l'encontre du principe fondamental de l'économie d'énergie, car la majorité des tortues marines vont migrer sur plusieurs centaines de kilomètres pour pondre dans une zone éloignée de leur milieu de vie.

Les tortues sont multiparentées et peuvent stocker le sperme de plusieurs mâles pendant plusieurs mois grâce à la présence de tubules de stockage du sperme (SST) dans l'oviducte des femelles (Gist & Jones, 1989; Kitayama et al., 2021). Il est généralement admis que la reproduction s'effectue au sein d'une même population, même s'il a été observé que les mâles peuvent se reproduire avec des femelles de populations adjacentes dans des zones dites « de contact » (FitzSimmons et al., 1997a, 1997b). Une fois la reproduction effectuée, les mâles retournent dans leurs zones d'alimentation (Chevalier, 2005). Les tortues marines pondent sur leur site de naissance tous les deux à sept ans (Lescure, 1987; Chevalier & Lartiges, 2001; Price et al., 2004; Chevalier, 2005). C'est généralement de nuit que les femelles vont rejoindre la plage, creuser un nid et pondre entre 50 et 130 œufs (Lutz & Musick, 1997). Les tortues marines sont classées comme ayant une stratégie de reproduction de type « r », elles ne prodiguent aucun soin à leur progéniture, mais elles pondent un grand nombre d'œufs afin de maximiser les chances de survie (Broderick et al., 2003; Calcagno, 2017).

Selon différents auteurs, le processus de nidification des tortues marines peut être décrit en 7, 9 ou 11 phases distinctes, communes aux diverses espèces et décrites de manière détaillée (Hailman & Elowson, 1992; Limpus et al., 1992). Toutefois, sept étapes principales sont généralement reconnues comme communes. La montée consiste à quitter l'eau et à remonter la plage jusqu'à un site de ponte choisi, avec des pauses fréquentes, et se déroule généralement la nuit. Une fois le site de ponte atteint, la phase de balayage débute, où la tortue forme une zone appelée « fosse corporelle » en projetant le sable à l'aide de ses membres antérieurs. Suis la phase de creusage, où les nageoires postérieures sont utilisées pour creuser une cavité cylindrique destinée aux œufs, qui sera plus ou moins profonde en fonction de la taille de la femelle. La ponte s'effectue dans un état de transe (Dutton, 1995), pendant lequel la femelle dépose les œufs dans la cavité creusée. Ensuite, elle rebouche le nid avec du sable et finit par le camoufler en dispersant du sable pour dissimuler le nid, créant parfois de faux nids. Enfin, la tortue retourne à l'eau rapidement. Au sein d'une même saison de ponte; les femelles vont revenir pondre plusieurs fois, soit tous les 10 à 15 jours, afin de permettre l'oviductogenèse (Gist & Congdon, 1998; Miller, 2017). Une fois leur saison de ponte terminée, les femelles repartent sur leurs zones d'alimentation côtières, ou pélagiques pour la tortue luth. Selon Hoekstra et al. (2020), les tortues marines présentent une sénescence démographique très lente. Aucune preuve n'indique un déclin reproductif marqué avec l'âge, suggérant qu'elles peuvent pondre jusqu'à leur mort.

1.2 La tortue luth

La tortue luth, *Dermochelys coriacea*, est la seule représentante actuelle du genre Dermochelys et de la famille des Dermochelyidae, apparue au Crétacé inférieur, il y a environ 100 et 150 millions d'années, ayant donc divergé des autres espèces de Cheloniidae, famille regroupant nos tortues marines actuelles (Pereira et al., 2017). Elle est l'espèce la plus imposante parmi les tortues marines et possède la plus grande répartition géographique de tous les reptiles actuels, étant seulement absente des mers Arctique et Antarctique (Pritchard & Trebbau, 1984; Fisheries and Oceans Canada, 2006). Elle mesure en moyenne deux mètres de long pour un mètre de large et pèse entre 300 et 900 kilos (Eckert & Luginbuhl, 1988). La tortue luth se distingue des autres tortues marines par plusieurs caractéristiques uniques. Contrairement aux autres espèces, elle ne possède pas d'écailles, car après quelques semaines de vie, les jeunes tortillons perdent leurs écailles présentes à la naissance (Eckert et al., 2012). À la place, la carapace est recouverte d'une épaisse peau noire-bleutée, d'aspect cuirassé, qui a donné son nom anglais à l'espèce "Leatherback turtle" (**Fig. 3**). Sous cette peau se trouvent de petites plaques osseuses appelées ostéodermes, particulièrement visibles le long des sept carènes qui parcourent leur dos (Chen et al., 2015). Sa face ventrale présente une teinte rosée, contrastant avec la coloration sombre du dos, et arbore sur le sommet du crâne une tache rose, appelée « tâche pinéale », unique à chaque individu (McDonald & Dutton, 1996). Les ostéodermes, composés d'hydroxyapatite et de collagène, assurent une fonction de protection tout en maintenant une flexibilité indispensable aux besoins respiratoires et de plongée de l'espèce (Chen et al., 2015). L'assemblage des ostéodermes assure une double fonction : protéger contre les prédateurs et permettre des mouvements en milieu aquatique. Cette architecture unique, caractérisée par des sutures ondulées, allie rigidité, résistance, flexibilité et stabilité (Chen et al., 2015).

Figure 3. Photographie d'une tortue luth à Salines (©Aquasearch).

La tortue luth présente des adaptations physiologiques remarquables pour vivre dans des environnements variés, notamment dans des eaux froides. Elle est un exemple de gigantothermie : sa grande taille, son isolation thermique efficace et sa capacité à réguler son flux sanguin lui permettent de maintenir une température corporelle stable (Paladino et al., 1990; Morreale et al., 1996). Cette espèce est capable d'atteindre des profondeurs de plongée de 1 200 mètres pour des durées dépassant les 60 minutes (Houghton et al., 2008), grâce à une morphologie souple et une carapace flexible adaptée aux fortes pressions hydrostatiques (Murphy, Kelliher et al., 2012). Malgré cette capacité à évoluer dans les eaux froides pour s'alimenter, ses activités de nidification restent limitées aux zones tropicales et subtropicales (Ferraroli et al., 2004; Hays et al., 2004, 2006; James et al., 2005; Dodge et al., 2014). La tortue luth est une espèce difficile à observer en raison de son mode de vie pélagique, de sa discrétion et de sa capacité de plongée (Houghton et al., 2008). On la retrouve dans les océans Atlantique, Pacifique et Indien, entre environ 71° de latitude nord et 47° de latitude sud. En Atlantique Nord, les tortues luth fréquentent particulièrement les eaux du Canada et du nord-est des États-Unis, comme le confirment les données de télémétrie satellitaire (James et al., 2005b; Eckert et al., 2006). Des agrégations saisonnières de tortues ont également été observées par des survols aériens et des données d'observateurs des pêches (Shoop & Kenny, 1992; Witzell, 1999). Dans l'Atlantique Nord-Est, les tortues luth se retrouvent aussi autour de la Grande-Bretagne et de l'Irlande (environ 50–60°N), et le record le plus au nord est celui d'une tortue nageant à 71°N, 23°E, au large de la Norvège (Carriol & Vader, 2002). En outre, des indices paléoécologiques suggèrent que la fréquentation des eaux tempérées par la tortue luth remonte à plus de 40 millions d'années (Albright et al., 2003).

L'alimentation de la tortue luth est spécialisée et constituée d'organismes gélatineux (Den Hartog & Van Nierop, 1984; Davenport & Balazs, 1991). Elle se nourrit principalement de méduses, notamment *Rhizostoma sp.*, *Chrysaora sp.* et *Cyanea capillata*, mais consomme également des salpes, du zooplancton, des crustacés et parfois des oursins (Bjorndal, 1997). Bleakney et *al*. (1965) suggèrent que les tortues s'aventurent dans les eaux au large du Canada pour exploiter les abondantes populations saisonnières de méduses. De plus, Nordstrom et *al*., (2020) ont trouvé une forte corrélation entre la distribution des tortues luth et celle des méduses sur le plateau néo-écossais (r = 0,89), ainsi que des corrélations modérées dans le golfe du Saint-Laurent et la baie de Fundy (r = 0,74).

Les tortues luth pondent en moyenne entre 6 et 11 fois par saison, à des intervalles de 8 à 11 jours, chaque nid contenant environ 70 à 80 œufs (Bell et al., 2004; Buonantony, 2008). Le dimorphisme sexuel est peu marqué chez la tortue luth. Elle ne possède pas de griffes sur les nageoires, contrairement aux autres tortues marines (Lutz et al., 2003; Wyneken, 2003). Cependant, les mâles présentent généralement un plastron plus concave et une taille légèrement supérieure, facilitant l'accouplement (Lutz et al., 2003; Wyneken, 2003). Contrairement aux autres espèces de tortues, elles nichent près de la zone de balancement des marées et montrent une fidélité relativement faible à leur site de ponte (Kamel & Mrosovsky, 2004; Horrocks et al., 2016). En effet, Horrocks et al (2016) ont suivi 3 151 femelles luth baguées entre 2002 et 2013, et ont montré que 211 ont été revues ailleurs à 240 reprises, sur 22 sites répartis dans 17 pays de la Caraïbe, avec 2,8 % de déplacements au sein d'une même saison de ponte et 4,3 % entre différentes saisons de ponte. Cette étude souligne surtout que certains individus présentent une faible fidélité à leurs sites de nidification. De plus, lors des suivis de ponte d'Aquasearch en 2025, une tortue en ponte et baguée à Grenade a été observée quelques jours plus tard en ponte sur la plage des Salines en Martinique (de Montgolfier, Comm. Pers.). Cette observation constituant une preuve supplémentaire de la non-fidélité au site de ponte chez certains individus.

L'estimation de l'âge à maturité varie de 12 à 20 ans (Dutton et al., 2005; Jones et al., 2011b). Comme les autres tortues marines, les tortues luth accumulent des réserves avant la reproduction et cessent de se nourrir durant cette période (Plot et al., 2013). La réussite d'éclosion est souvent inférieure à 50 % à l'échelle mondiale (Perrault et al.,, 2012) et est sensible aux conditions climatiques, notamment aux fortes pluies et aux tempêtes entrainant de la houle et une montée du niveau de la mer (Houghton et al., 2007; Santidrián Tomillo et al., 2015).

Malgré ses adaptations uniques, la tortue luth est aujourd'hui menacée. Autrefois très répandue, cette espèce a vu ses effectifs s'effondrer, notamment dans le Pacifique où les populations de certaines régions, comme en Malaisie, ont totalement disparu, tandis que celles du Mexique et du Costa Rica ont connu une chute vertigineuse dans les années 1990 (Spotila et al., 2000). Cette régression s'expliquerait par le fort taux de braconnage des œufs et la capture accidentelle par les engins de pêche (Spotila et al., 1996). Spotila et al. (2000) soulignent que la mortalité des adultes en mer, notamment à cause des pratiques halieutiques, constitue aujourd'hui une menace majeure, au point que près de 90 % des femelles reproductrices du Pacifique ont disparu au cours des vingt dernières années (COSEPAC, 2012). Pour répondre à cette urgence, diverses initiatives ont vu le jour, comme l'accord IOSEA pour la protection des tortues marines et de leurs habitats (CMS, 2001). En 1979, la tortue luth fut inscrite sur l'Annexe I et II de la Convention sur les espèces migratrices (CMS) qui permet une coopération internationale renforcée (CMS, 1979). Actuellement, elle est classée « Vulnérable » par l'Union Internationale pour la Conservation de la Nature (UICN), bien que certains pays, comme le Canada et la France (dont la Martinique fait partie), l'aient respectivement classée comme « En voie de disparition » et « En danger » (COSEPAC, 2001; DEAL, 2020).

1.3 La tortue imbriquée

La tortue imbriquée, *Eretmochelys imbricata*, est la seule espèce du genre Eretmochelys, et appartient à la Famille des Cheloniidae (**Fig. 4**). Des analyses de leur ADN mitochondrial révèlent deux lignées principales : Atlantique et Indopacifique dus à des dispersions sur de longues distances depuis le Pliocène (Arantes et al., 2020). La tortue imbriquée mesure en moyenne 70 à 95 cm de longueur de carapace, pour 45 à 85 kilos avec des spécimens exceptionnels atteignant jusqu'à 127 kg (Meylan & Donnelly, 1999; Mortimer & Donnelly, 2008). Elle se distingue par sa carapace elliptique, fortement carénée, recouverte de larges écailles osseuses imbriquées, d'où elle tire son nom, lui conférant une forte robustesse (Witzell, 1983). Sa tête est relativement petite avec un bec crochu caractéristique (Bjorndal et al., 1997). La coloration de la carapace présente un motif complexe de teintes orangées, brunes et noires, qui joue un rôle crucial dans le camouflage au sein des récifs coralliens (Meylan, 1988). De plus, sa morphologie hydrodynamique, notamment la forme allongée de ses membres antérieurs, optimise ses déplacements dans l'eau. Le dimorphisme sexuel de cette espèce est bien marqué par la présence de griffes très développées chez les mâles, ainsi que leur plastron concave et leur queue plus développée (Witzell, 1983) avec une maturité sexuelle tardive entre 23 et 36 ans (Snover et al., 2013).

Figure 4. Photographie de tortue imbriquée à Saint Eustache (©Stenapa, 2023).

La tortue imbriquée est circumtropicale, elle vit généralement entre les latitudes 30°N et 30°S (Baillie & Groombridge, 1996) et pond dans plus de 60 pays (Groombridge & Luxmoore, 1989). Toutefois, dans la Caraïbe, cette espèce forme de petites agrégations de nidification, plutôt faibles en densité (Piniak & Eckert, 2011). On la retrouve proche de récifs coralliens peu profonds où elle se nourrit essentiellement d'éponges, mais aussi d'anémones, de mollusques et de crustacés (Meylan, 1988). Du fait d'une alimentation riche en éponges marines, cette tortue a pour particularité d'avoir une chair toxique (Pavlin et al, 2015). La période inter-nidification moyenne des femelles imbriquées est d'environ 17,4 ±7,1 jours (Gulick et al., 2022). Durant chaque saison de reproduction, les femelles déposent en moyenne 142,8 ± 28,9 œufs à chacune des 3 à 5 pontes, bien que ce nombre puisse varier selon l'âge, la condition physique et la qualité des zones d'alimentation (Richardson et al., 1999; Gulick et al., 2022). Quant au taux d'éclosion des œufs, il varie généralement entre 60 % et 85 %, selon les régions, la qualité de l'habitat de nidification, et les conditions environnementales (Bjorndal et al., 1985; Mortimer & Bresson, 1999). Plusieurs études ont démontré que cette espèce présente un comportement de philopatrie, les femelles retournant de manière récurrente sur leur site de naissance pour y pondre (Bowen & Karl, 1997; FitzSimmons et al., 1997b; Levasseur et al., 2019). Bien qu'elles aient pu, durant leur phase juvénile, s'alimenter dans des habitats de croissance idéaux et abritant les nids d'autres femelles, ces tortues vont migrer sur des centaines voire des milliers de kilomètres afin de rejoindre leur plage de ponte (Mortimer, 2000) puis repartir sur leurs aires d'alimentation.

Les estimations mondiales suggèrent qu'il reste entre 20 000 et 23 000 femelles reproductrices (NMFS & USFWS, 2013; Bustard, 2016), avec environ 8 000 individus dans les populations les plus importantes (NOAA Fisheries, 2025). Au cours des cent dernières années, la population mondiale de tortues imbriquée a diminué de plus de 80 % (Mortimer & Donnelly, 2008; Martínez-Estévez et al., 2023). Malgré ces chiffres faibles, certaines populations montrent des signes de récupération lente, en particulier dans les Caraïbes (NOAA Fisheries, 2025). Toutefois, une légère baisse de la taille moyenne des femelles, de la taille des pontes, ainsi que des taux d'éclosion et d'émergence a été constatée au cours de la dernière décennie (López Castro et al., 2022). Ces évolutions, bien qu'encore non significatives sur le plan statistique, semblent corrélées à des facteurs environnementaux tels que le réchauffement des océans et les perturbations des régimes écologiques, qui altèrent la productivité marine et réduisent la disponibilité en nourriture dans les zones d'alimentation (Poloczanska et al., 2009; Stephenson, 2014). Par ailleurs, des recherches menées sur la tortue Caouanne (*Caretta caretta*) ont montré que l'origine des zones d'alimentation influence de manière significative la taille des pontes et la fréquence de reproduction (Vander Zanden et al., 2014), suggérant que les disparités de qualité entre habitats trophiques pourraient également expliquer les tendances observées chez les tortues imbriquée dans cette région. Les tortues imbriquées de l'Atlantique Ouest ont vu leurs taux de croissance diminuer de 26 % entre 1999 et 2015, principalement à cause d'un changement écologique majeur lié au El Niño de 1997/98 et au réchauffement des eaux de surface (Bjorndal et al., 2017). Ce bouleversement a réduit la productivité primaire marine, affectant la disponibilité alimentaire et ralentissant la croissance des tortues (Bjorndal et al., 2017). La tortue imbriquée fut classée « en danger » en 1968 par l'UICN puis placée sur la liste rouge en 1996 en tant qu'espèce « en danger critique » (Baillie & Groombridge, 1996). La tortue imbriquée a été inscrite en 1975 aux annexes de la CITES, avec la population de l'Atlantique classée en Annexe I et celle du Pacifique initialement en Annexe II, puis reclassée en Annexe I en 1977. Elle figure également aux Annexes I et II de la CMS (IUCN Species Survival Commission, 1994; Baillie & Groombridge, 1996).

2. SITE D'ÉTUDE

Les Caraïbes sont considérées comme un « hotspot » de biodiversité en raison du niveau élevé d'endémicité et de menaces (Myers et al., 2000; Wege et al., 2010; Hrdina & Romportl, 2017). Cette région est capitale pour la conservation des tortues marines car elle héberge des sites de ponte, d'alimentation et de migration essentiels pour toutes les espèces, hormis la tortue à dos plat (*Natator depressus*) endémique du nord de l'Australie (Walker & Parmenter, 1990). La diversité des habitats caribéens, des plages sableuses aux herbiers marins et aux récifs coralliens, confère à cette région une importance stratégique capitale pour l'ensemble du cycle de vie des tortues marines. Trois des quatre sites de ponte majeurs de tortues luth s'y trouvent : le Costa Rica (côte caribéenne), les Guyanes (Guyane française et Suriname) et Trinidad. La quatrième se situant au Gabon (Troëng et al., 2007; Fossette et al., 2008). La côte caribéenne du Costa Rica se distingue par des taux de fréquentation record pour la tortue luth, avec une densité moyenne de 142 nids/km et un taux d'éclosion moyen de 55 % ± 6 % (Rivas et al., 2016). Les tortues luth des autres sites des Caraïbes, en revanche, semblent bénéficier d'un succès d'éclosion plus élevé et d'une incidence moindre de la prise accessoire par les pêcheries, expliquées par une nidification plus dispersée et un chevauchement réduit entre les zones de pêche et les habitats des tortues (Troëng et al., 2007). Par ailleurs, la tortue de Kemp, l'espèce de tortue la plus menacée selon l'UICN, concentre la quasi-totalité de sa ponte sur la plage de Rancho Nuevo au Mexique, avec quelques événements rares à Padre Island (Texas, USA). Les résultats de l'étude de Balladares et *al.*, (2024) soulignent que les Caraïbes représentent un axe spatial crucial, en particulier pour les tortues imbriquées. Ce corridor marin relie d'importantes plages de ponte (de Puerto Rico à la côte Vénézuélienne), permettant à ces tortues de migrer sur des distances de plusieurs milliers de kilomètres entre les sites de reproduction, les zones d'alimentation et les aires de croissance. Cette connectivité transfrontalière démontre que la préservation des habitats dans toute la région Caraïbe est essentielle pour la survie de ces espèces. Ainsi, la préservation des tortues marines dans les Caraïbes exige des efforts de conservation transfrontaliers et une coopération régionale renforcée, incluant la protection des grands sites de nidification (Thomé et al., 2007).

2.1 La Martinique

Située dans les Petites Antilles, la Martinique est une île volcanique française d'une superficie de 1 128 km² (**Fig. 5**). Entourée par la mer des Caraïbes à l'Ouest et l'Océan Atlantique à l'Est, cette île de 355 500 habitants (Insee, 2025) possède un climat de type tropical humide (Portecop, 1978). Le climat local est marqué par deux saisons principales : une période sèche s'étendant de janvier à mai, suivi d'une saison des pluies de juin à décembre qui coïncide avec la saison cyclonique (Météo France, 2020). Depuis plusieurs années, différents acteurs tentent d'établir des bases de données afin de mieux évaluer l'évolution de la ponte et d'identifier les principaux sites de nidification de l'île. Ainsi, 138 sites ont été sélectionnés en Martinique, dont 113 ont été confirmés par la nidification de tortues (DEAL Guadeloupe, 2018). Au nord de l'île, les plages arborent un sable sombre, issu de l'activité volcanique, plus présente à l'extrémité nord. Un gradient s'observe ensuite vers le sud, où le sable passe à une texture fine et une couleur blanche.

Figure 5. La Martinique et sa situation géographique.

Trois espèces de tortues marines pondent sur les plages de la Martinique. La tortue imbriquée est la plus abondante, principalement entre juin et octobre. La tortue luth, qui connaît un pic d'activité entre avril et juin, est également présente (Chevalier & Lartiges, 2001). La tortue verte, plus rare, est observée occasionnellement. Depuis 1993, les tortues marines sont protégées en Martinique. Leur vulnérabilité, confirmée par leur inscription sur la Liste Rouge de l'UICN, a conduit à l'adoption de mesures nationales de conservation dès 2006. L'arrêté ministériel du 14 octobre 2005 (Ministère de l'Écologie et du Développement durable, 2005) les reconnait comme espèces protégées en France. Un Plan National d'Action (PNA) dédié aux tortues marines des Antilles françaises a été lancé en 2008 (Crillon & Cuzange, 2018). Coordonné depuis 2017 par l'ONF et géré par la DEAL, ce plan vise à surveiller les populations, restaurer les habitats et sensibiliser le public (Crillon & Cuzange, 2018).

Dans le cadre de ce mémoire, nous avons centré nos études et suivi sur trois plages, identifiées comme des sites majeurs de nidification en Martinique : Madiana, Le Diamant et Les Salines. Ces sites ont été sélectionnés en raison de leurs niveaux contrastés d'anthropisation, de la diversité de leurs habitats et de leur couverture végétale, ainsi que de leur répartition géographique sur l'île.

2.1.1 Madiana

Située à seulement 3 km de Fort-de-France, la capitale, dans la ville de Schoelcher, la plage de Madiana (14°36'43"N 61°05'54"W) mesure 200 m de long et est considérée comme notre site le plus perturbé par l'activité anthropique (**Fig. 6**). Se trouvant sur la côte caraïbe, elle est composée de sable gris-noir hérité de l'activité volcanique du nord de l'île. Très fréquenté de jour comme de nuit, on y retrouve un restaurant en arrière-plage, des terrains de volley ayant un éclairage puissant allumé tous les soirs jusqu'à environ 22h, et une activité de pêche régulière (lignes et sennes). La végétation ne couvre qu'environ 1/4 de cette plage, et la largeur du banc de sable varie entre 0 et 25 mètres. Enfin, on peut relever la présence importante de potentiels prédateurs tels que des chiens et chats errants, des crapauds-bœufs (*Rhinella marina*), des rats (*Rattus norvegicus* et *Rattus rattus*) et des crabes fantômes (*Ocypode quadrata*). On retrouve essentiellement des tortues imbriquées en ponte sur la plage de Madiana avec une exception, une ponte de tortue luth en 2025. Du fait de sa petite taille, et du manque de sites de ponte adaptés (peu de végétation et de zones ombragées), le déterrement de nids par d'autres femelles a déjà été observé à de multiples occasions, par les équipes de suivi des pontes.

Figure 6. Vu satellitaire de la plage du Diamant et une photographie (©Chloé Vanleynseele).

2.1.2 Diamant

La plage du Diamant (14°28'32"N 61°02'10"W), située sur la côte Caraïbe dans la commune homonyme, est l'une des plus connues et fréquentées de Martinique (**Fig. 7**). Elle s'étend sur 2,5 km de long, avec une largeur variant de 10 à 20 m. Les zones sableuses représentent environ 9 % de la surface, les rochers/enrochements 10 %, tandis que la végétation dense et moyennement dense couvre 34 %, avec une répartition équilibrée (de Montgolfier, Comm. Pers.). On y retrouve des zones urbanisées aux deux extrémités, avec à l'est un restaurant en bord de plage lumineux jusqu'à 1h du matin puis un enchainement de propriétés privées. De l'autre côté, on y retrouve des constructions (marché et habitations). Toutefois, le centre de la plage, d'environ 1,2 km, est sombre grâce à une forêt plutôt dense, idéale pour la ponte des tortues imbriquée (de Montgolfier, Comm. Pers.). Des recensements débutés en 2020 ont relevé trois espèces de tortues nichant sur la plage du Diamant : la tortue imbriquée, la tortue luth et, plus occasionnellement, la tortue Verte. N'ayant rencontré qu'une tortue Verte au cours des 4 années de suivi sur lesquelles se base ce mémoire, nous ne l'avons pas prise en compte dans nos études. La plage du Diamant abrite également de nombreux crabes fantômes (*Ocypode quadrata*) et crabes touloulou (*Gecarcinus lateralis*). Cette plage subit des échouages massifs de sargasses (*Sargassum fluitans* et *Sargassum natans*). La plage du Diamant est considérée comme ayant un niveau de perturbation anthropique intermédiaire grâce à sa longue zone centrale peu exposée à l'activité humaine la nuit.

Figure 7. Vu satellitaire de la plage du Diamant et une photographie (©Jessie-Lee Langel).

2.1.3 Salines

Relativement isolée des aires urbaines, la plage des Salines (14°24'14"N 60°52'47"W) est située dans la commune de Sainte-Anne (**Fig. 8**). C'est notre plage la moins impactée par les activités anthropiques du fait de son isolement géographique. Elle s'étend sur environ 1,3 km de long et 20 à 40 m de large sur la côte sud de la Martinique. Elle possède une fréquentation assez élevée en journée lors de la saison touristique en raison de son sable blanc. Cette plage est composée d’environ 25 % de zone sableuse, et d’une large zone boisée longeant la plage (de Montgolfier, Comm. Pers.). Il peut arriver des épisodes d’échouage de Sargasses (*Sargassum fluitans* et *Sargassum natans*), mais ces évènements sont relativement peu importants. Elle est aussi connue pour être sujette à l’érosion côtière (Dolique et al., 2019). Aucune lumière artificielle n’est présente sur cette plage et elle est rarement fréquentée de nuit. Tout cela en fait un site de ponte idéal pour la tortue imbriquée et la tortue luth. Parmi les potentiels prédateurs des jeunes tortues, on retrouve une forte abondance de crabes fantômes (*Ocypode quadrata*) et de touloulous (*Gecarcinus lateralis*), et la présence de mangoustes (*Urva auropunctata*) et de chats errants.

Figure 8. Vu satellitaire de la plage des Salines et une photographie (©Jessie-Lee Langel).

3. MENACES ET ENJEUX

Les tortues marines figurent aujourd'hui parmi les espèces les plus menacées de la planète. Leur cycle de vie complexe, leur dépendance à divers écosystèmes marins et côtiers, et leurs longues migrations les exposent à une multitude de menaces. Le taux de survie est estimé à 1 œuf sur mille, soit la production d'une seule femelle et un mâle par génitrice en moyenne (Frazer, 1986). Les pressions exercées sur les tortues marines sont à la fois naturelles et anthropiques, directes ou indirectes, locales ou globales.

3.1 Pressions naturelles

La première menace que subissent les tortues est la prédation dès leur naissance (Temple, 1987; Caut et al., 2006; Leighton et al., 2011; Louppe et al., 2021) limitant le nombre d'individus atteignant l'âge adulte. La prédation est souvent présente aux toutes premières heures de vie des tortillons, causée par les oiseaux, les crabes (*Ocypode sp.*; *Gecarcinus lateralis*), la mangouste (*Urva auropunctata*), le rat (*Rattus rattus*; *Rattus norvegicus*), le chat (*Felis catus*) ou encore le chien (*Canis lupus*) (Butler et al., 2020; Stokes et al., 2024). Cependant, le braconnage est aussi une menace que rencontrent les tortues à tous leurs stades de vie (Aguirre & Nichols, 2020). Une menace naturelle est l'hybridation, dont plusieurs cas ont été rapportés. La tortue imbriquée semble la plus concernée notamment des cas d'hybridation avec la tortue Caouanne (*Caretta carreta*) (Lara Ruiz et al., 2006; Arantes et al., 2020), la tortue Verte (*Chelonia mydas*) (Restrepo et al., 2022) et la tortue Olivâtre (*Lepidochelys olivacea*) (Lara-Ruiz et al., 2006). Ces hybrides F_1 se reproduisent, mais possèdent un succès de nidification significativement inférieur aux espèces parentales, illustrant un effet de croisement éloigné et une baisse de résilience démographique (Arantes et al., 2020). Ces observations suscitent deux préoccupations majeures : d'une part, l'introgression génétique menace l'intégrité des espèces menacées, d'autre part, le succès reproductif réduit des hybrides pourrait affaiblir les populations locales déjà menacées (Vilaça et al., 2023).

3.2 Menaces anthropiques indirectes

Le climat a toujours exercé une forte influence sur les populations de tortues marines, en particulier le recrutement. Ainsi l'augmentation des températures, l'accélération de la montée du niveau des mers et l'augmentation des événements climatiques extrêmes attribuable aux activités humaines impactent les populations de tortues (Hawkes et al., 2009; IPCC, 2019; Santidrián Tomillo et al., 2020). La température du sable lors de la maturation des œufs joue un rôle majeur dans le développement et la viabilité des embryons (Santidrián Tomillo et al., 2009; Fuentes et al., 2011; Lolavar & Wyneken, 2015; Laloë et al., 2017; Lolavar & Wyneken, 2017). En effet, le sexe des embryons étant déterminé par la température du nid, l'équilibre sex-ratio des espèces de tortues marines est menacé par le réchauffement global en plus de la disparition des zones boisées qui produisaient de l'ombrage, et donc des zones plus fraiches pour les nids (Janzen, 1994; Esteban et al., 2018).

L'intensification des pluies affecte négativement le succès d'émergence des tortues (McGehee, 1990; Houghton et al., 2007; Balladares et al., 2022). De plus, le changement climatique entraine également une intensification et une précocité des ouragans qui détruisent les nids et modifient le littoral (**Fig. 9**) (Wang & Wu, 2004; Kamel & Delcroix, 2009; Fuentes et al., 2019; Langel et al., 2024). Ils s'ajoutent à une érosion côtière déjà bien présente à cause de l'élévation du niveau de la mer et qui réduit les zones de nidification (Bosser et al., 2000; Fish et al., 2008; Schleupner, 2008; Witherington et al., 2011; Fujisaki et al., 2018).

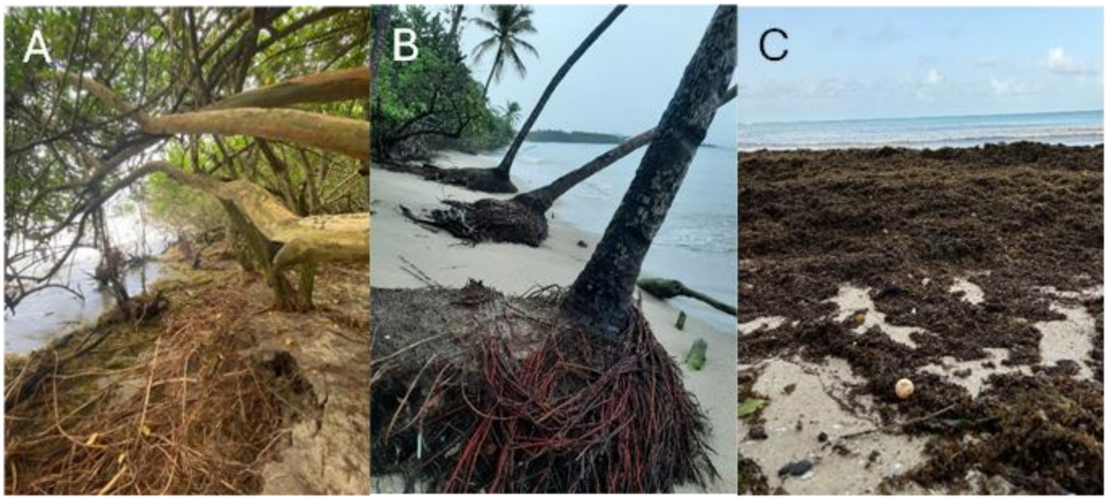

Figure 9. Impact de l'ouragan Beryl sur la plage du Diamant (A) et Salines (B, C). On observe une disparition de la partie sableuse de la plage du Diamant et une accumulation de Sargasses ainsi que des œufs jonchant le sol sur la plage des Salines.

Une problématique également liée au changement climatique, et qui est très présente dans l'Atlantique et les Caraïbes, est l'échouage de Sargasses (*Sargassum fluitans* et *Sargassum natans*) qui empêche les femelles de monter pondre sur les plages, et peut étouffer les nids et les juvéniles au moment de leur émergence (**Fig. 10**; Gower et al., 2013; Djakouré et al., 2017; Louime et al., 2017; Maurer et al., 2021; Maurer et al., 2022). Toutefois, il a été démontré que les échouages de Sargasses pourraient agir comme barrière naturelle et empêcher, partiellement, l'érosion de certaines plages (Mantran et al., 2023). Enfin, les modifications du climat perturbent les réseaux trophiques marins, pouvant potentiellement réduire l'abondance de proies telles que les herbiers, essentiels aux tortues Verte, ou les invertébrés consommés par les juvéniles et adultes (Hamann et al., 2007; Wyneken & Salmon, 2020). Ces contraintes combinées pèsent lourdement sur le taux de survie dès les premiers stades de vie, affaiblissant potentiellement les populations de plusieurs espèces.

Figure 10. Plage de Zeelandia (Sint Eustatius) touché par les échouages de Sargasses même en l'absence de tempêtes (©Jessie-Lee Langel).

3.3 Menaces anthropiques directes

De nos jours, 42 pays autorisent encore la pêche de tortues marines. Selon Humber, Godley et Broderick (2014), la pêche légale des tortues marines a fortement diminué depuis les années 1980, passant de 120 000 à environ 42 000 captures par an grâce aux lois de protection et aux efforts de conservation. Toutefois, elle persiste dans certains pays pour des raisons alimentaires, culturelles ou économiques, en particulier pour la consommation de viande de tortue Verte (Senko et al., 2022). La pêche accidentelle représente un autre facteur de mortalité non négligeable. Lors des opérations de pêche industrielle ou artisanale, de nombreuses tortues se retrouvent piégées dans les filets et meurent noyées (Spotila et al., 2000). De plus, la pêche fantôme, c'est-à-dire les filets abandonnés dérivant en mer, continue de tuer de nombreux individus (Wallace et al., 2010). Ces impacts sont d'autant plus critiques que les tortues parcourent de vastes distances et partagent des aires d'alimentation communes, ce qui fait que la mortalité dans une zone donnée peut affecter des populations provenant de colonies très éloignées (Ferraroli et al., 2004; Bowen et al., 2005). Dans certains pays où la pêche et la consommation de tortues marines sont officiellement interdites, on retrouve toujours un braconnage parfois intense. La tortue imbriquée est particulièrement ciblée, notamment pour sa carapace, utilisée dans la fabrication de bijoux et d'objets décoratifs depuis le XV^{e} siècle (Parsons, 1972). Bien que le commerce international de ces produits soit aujourd'hui largement interdit par la CITES, une partie du commerce reste active, notamment entre pays non-signataires, ou à travers des marchés informels (Senko et al., 2022). Le braconnage des œufs constitue une autre menace majeure. Dans plusieurs régions, les œufs sont consommés pour leurs vertus supposées ou comme met traditionnel, ce qui induit une pression persistante sur les plages de ponte (Chacón et al., 1996; Troëng, 2000). Dans certains cas, ce braconnage est si intense qu'il compromet directement la viabilité des populations locales. À Tortuguero, au Costa Rica, un déclin de 77 à 95 % des effectifs a été documenté, principalement attribué à la collecte illégale des œufs et à la chasse des femelles nicheuses (Troëng et al., 2005). Enfin, la demande persistante d'écailles de tortue, assimilée à celle de produits de luxe comme l'or ou l'ivoire, reste une incitation économique forte au braconnage, malgré les interdictions officielles (Chevalier & Girondot, 2000; Senko et al., 2022). La collecte d'œufs, souvent liée à des traditions culturelles enracinées, ne montre pas de signes de recul non plus dans certaines zones (Pheasey et al., 2020).

La survie des espèces de tortues est fortement liée à la qualité de leurs sites de nidification. Toutefois ces derniers subissent des perturbations majeures telles que l'introduction de prédateurs, l'urbanisation côtière, l'élévation du niveau de la mer et l'intensification du tourisme (Pavis et al., 2004; Fish et al., 2008; Comité français de l'UICN & ONCFS, 2011). L'urbanisation modifie et réduit les sites de ponte, en limitant les espaces forestiers naturels (Fuentes et al., 2016; Magdic, 2021). Une étude effectuée sur une grande partie des pays de la Mer des Caraïbes indique que 20 % des plages historiques de ponte ont disparu et que 50 % des sites restants sont gravement menacés (McClenachan et al., 2006). L'artificialisation des plages est une problématique globale. L'éclairage artificiel en est un exemple emblématique, car il désoriente les tortillons qui suivent le point le plus lumineux censé les apporter vers l'eau (Claro & Bardonnet, 2011; Oliver de la Esperanza et al., 2017; Guy, 2020). À l'échelle mondiale, les zones côtières attirent 50% des touristes (UNWTO, 2013). Le tourisme est donc un acteur majeur de l'économie des populations côtières. Toutefois, toutes ces activités humaines concentrées aux mêmes endroits entrainent un surplus de bruits, de piétinements et perturbent le comportement des femelles en ponte, favorisant ainsi une hausse des échecs de ponte (Godley et al., 2001; Wilson & Tisdell, 2001; Mrosovsky et al., 2002; Oliver de la Esperanza et al., 2017).

Les tortues marines sont aujourd'hui confrontées à de nombreuses menaces liées à la pollution marine, notamment l'accumulation de polluants chimiques dans leur habitat. Parmi ces polluants, on retrouve les métaux lourds comme le mercure (Hg), le plomb (Pb), le cadmium (Cd), l'arsenic (As) ou encore le zinc (Zn), qui sont bioaccumulés par les tortues (Caurant et al., 1999; Ross et al., 2017; Yipel et al., 2017; Dennis et al., 2020; Hrizi et al., 2024). Plusieurs études ont démontré également un transfert des polluants de la mère aux tortillons (Godley et al., 1999; Guirlet et al., 2008; Ehsanpour et al., 2014; Dennis et al., 2020). Les contaminants organiques persistants, tels que les composés organochlorés comme les PCB, ainsi que les hydrocarbures issus du pétrole brut ou des hydrocarbures aromatiques polycycliques (HAP), représentent également une menace directe pour la santé des tortues marines (Van de Merwe et al., 2010; Stewart et al., 2011; Dyc et al., 2015). Hutchinson & Simmonds (1992) ont proposé un lien entre l'exposition chronique à ces composés et l'apparition accrue de la fibropapillomatose, une maladie virale touchant principalement les tortues marines, caractérisée par l'apparition de tumeurs cutanées et parfois internes, pouvant gêner leur vision, leur mobilité ou leur alimentation. Même si cela reste une menace minime au vu de l'importance de toutes celles citées précédemment, les cas de marées noires peuvent avoir un impact sur les populations de tortues concernées. Différentes études ont compilé les effets d'une telle exposition et ont relevé une augmentation de la mortalité embryonnaire, des malformations congénitales, de la mortalité directe des juvéniles et des adultes, des lésions de la peau, des altérations du système digestif, immunitaire et des glandes à sel, d'exfoliation cutanée, de troubles respiratoires et de déséquilibres métaboliques chez des tortues juvéniles exposées à des nappes de pétrole (Fritts & McGehee, 1982; Lutcavage et al., 1995; Milton et al., 2003). De même, Fritts et McGehee (1982) ont montré que des œufs incubés dans du sable contaminé présentaient des retards d'éclosion, des anomalies morphologiques et un taux de succès d'incubation nettement diminué.

3.4 Contraintes à la conservation et défis scientifiques

L'une des difficultés globalement rencontrées lors de l'étude des populations de tortues marines est la surestimation des populations. En effet, encore à l'heure actuelle, les comptages officiels s'effectuent en dénombrant le nombre de femelles pondeuses observées sur les plages (Santos et al., 2021). Toutefois, cette technique ne prend pas en compte la remigration intrasaisonnière des femelles qui peuvent venir pondre plus de 10 fois, selon l'espèce, sur une même période (Girondot & Fretey, 1996). Ainsi, on observe une surestimation et un manque de données pour les mâles. Tout ceci contribue à une difficulté dans la prise de décision et possiblement à un sous-classement dans les protections. De plus, les tortues parcourant des milliers de kilomètres entre leurs sites de ponte et leurs zones d'alimentation, il est donc difficile de cartographier précisément leurs routes migratoires, ce qui complique la mise en œuvre de mesures de protection en haute mer ou dans des zones transfrontalières nécessitant une forte coopération internationale.

Afin de pallier ces différentes problématiques, les scientifiques tentent de trouver des moyens innovants et les moins invasifs possibles. On peut citer comme exemple le suivi satellitaire utilisant des balises GPS ou « PIT tag » généralement placées sous la peau, dans la ceinture scapulaire antérieure ou directement sur le dos des femelles lors de leur ponte, ou des mâles capturés en mer. Toutefois, Hays & Hawkes (2018) mettent en avant des difficultés liées aux coût et à la durée de fonctionnement des balises, aux biais de représentativité, et à l'interprétation des données. Ils appellent à la diversification les approches méthodologiques pour réduire les possibles biais. La photo-identification (photoID) est également une technique de plus en plus utilisée par les scientifiques, permettant d'identifier chaque individu rencontré (**Fig. 11**) (McDonald & Dutton, 1996; Reisser et al., 2008; De Zeeuw et al., 2010; Calmanovici et al., 2018; Dunbar et al., 2021). Toutefois, cette méthode requiert un effort d'échantillonnage important et est sujette à différents biais, notamment la qualité de l'image, ainsi que l'efficacité du logiciel d'analyse et les compétences de l'utilisateur (Dunbar et al., 2014; Calmanovici et al., 2018; Steinmetz et al., 2018).

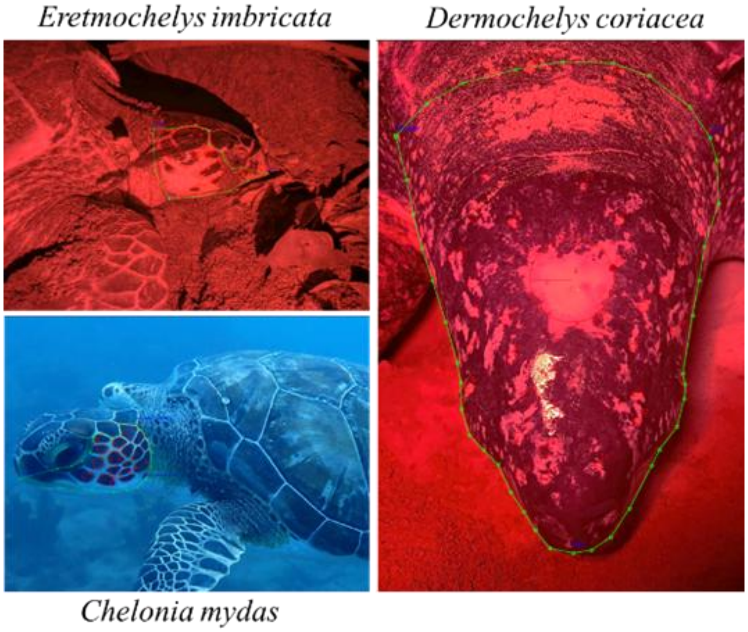

Figure 11. Utilisation du logiciel I3SPattern sur les tortues marines (©Aquasearch ©Stenapa).

Enfin, L'ADN environnemental (ADNe) est aujourd'hui un outil précieux pour étudier les populations de tortues marines sans avoir à les capturer, ce qui est particulièrement important pour ces espèces vulnérables et difficiles à observer (Thomsen & Willerslev, 2015; Harper et al., 2020; Farrell et al., 2022). Parallèlement, la métagénomique permet d'analyser le biofilm présent sur la carapace et la peau des tortues (**Fig. 12**). Des études ont montré que la composition de ce biofilm change en fonction des habitats fréquentés, servant ainsi de méthode pour mieux comprendre les déplacements et les interactions des tortues avec leur milieu naturel (Kanjer et al., 2022; Loghmannia et al., 2023). Le biofilm ne reflète pas seulement l'environnement dans lequel évolue la tortue, mais pourrait également donner des indications sur son état de santé général (Rivera et al., 2018; Filek et al., 2023). Toutefois, cette relation demeure encore peu étudiée, ce qui en fait un champ de recherche relativement préliminaire. L'ensemble de ces méthodes permettent d'envisager des études de population à large échelle et de mieux comprendre les dynamiques migratoires de ces espèces, même si l'utilisation de ces techniques d'analyse reste peu appliquée aux tortues marines.

Figure 12. Tortue luth au large de Saint Pierre et Miquelon couverte de biofilm (©Thierry Vogenstahl).

Malgré les nombreuses pressions que subissent les tortues marines (**Fig. 13**), elles sont aujourd'hui reconnues comme des espèces bio-indicatrices de la santé des écosystèmes marins (Hays et al., 2004). Leur large répartition géographique et leur longévité les exposent à une grande diversité de stress environnementaux, ce qui en fait des témoins privilégiés de la qualité de leur habitat. Plusieurs études scientifiques récentes ont démontré leur utilité pour suivre l'état de santé des océans, notamment en ce qui concerne la pollution plastique, la contamination chimique, la présence de bactéries résistantes aux antibiotiques, ou encore les variations dans les chaînes alimentaires. Par exemple, des recherches menées par Duncan et al. (2024), ont montré que 42,7 % des tortues Caouanne (*Caretta caretta*) de Méditerranée orientale avaient consommées des macroplastiques, mettant en lumière la pollution plastique de cette région.

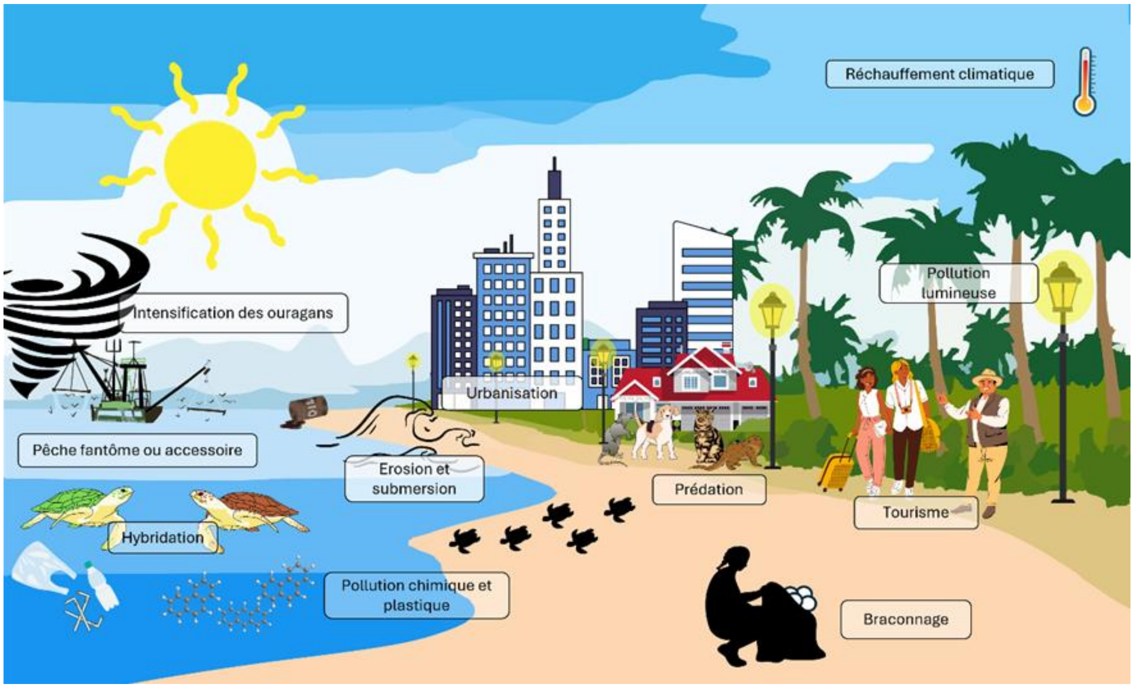

Figure 13. Résumé illustré des principales menaces pesant sur les tortues marines.

4. OBJECTIFS ET HYPOTHÈSES

L'objectif principal de cette étude est de caractériser la santé des populations de tortues en ponte sur trois plages de la Martinique, à l'aide de différents outils de suivi. Pour y répondre, trois objectifs spécifiques ont été définis, chacun constituant un chapitre de thèse :

1) Mesurer l'impact de l'ouragan Beryl survenu le 1er juillet 2024, lors de notre suivi annuel des pontes. L'hypothèse initiale est que cet ouragan aura un impact particulièrement néfaste sur la population de tortues luth et imbriquée pondant en Martinique au vu de sa précocité et de son intensité.

2) Définir le comportement des femelles pondeuses et l'influence de l'environnement sur leur nidification en utilisant la photo-identification comme moyen de discriminer chaque individu. Nous avons émis l'hypothèse que l'activité anthropique et l'habitat influencent le comportement de ponte des femelles et que la photoID permet d'estimer des différences interspécifiques en plus d'améliorer les estimations des populations.

3) Évaluer le potentiel de nouveaux outils, tels que la métagénomique du biofilm présent sur les carapaces et l'analyse de la composition en métaux des coquilles d'œufs, en tant qu'indicateurs des déplacements individuels. L'hypothèse sous-jacente est que la composition microbienne du biofilm et le profil métallique des coquilles pourraient refléter les environnements traversés par les femelles au cours de leurs migrations alimentaires. Ainsi, les variations observées entre individus d'une même plage, entre différentes plages, et entre espèces pourraient témoigner de la diversité de leurs déplacements. L'utilisation d'une approche multimarqueurs permettra de confirmer ou d'infirmer la capacité de ces indicateurs à discriminer l'hétérogénéité des trajectoires migratoires.

CHAPITRE 1

IMPACT DE L'OURAGAN PRÉCOCE BERYL SUR LA NIDIFICATION DES TORTUES MARINES EN MARTINIQUE

1.1 RESUMÉ

Les pays du bassin caribéen sont régulièrement soumis à des événements climatiques intenses tels que les ouragans. Début juillet 2024, l'ouragan Beryl est devenu le plus précoce ouragan de catégorie 4 jamais enregistré, frappant la Martinique avec une intensité sans précédent. Ces phénomènes météorologiques extrêmes constituent une menace importante pour le succès reproducteur des tortues marines menacées des Caraïbes. L'objectif principal de cette recherche est de déterminer l'impact direct de l'ouragan Beryl sur les populations nicheuses de tortues luth (*Dermochelys coriacea*) et de tortues imbriquées (*Eretmochelys imbricata*). Nous avons estimé les différents traits de côtes afin d'évaluer l'évolution du niveau de la mer, de l'intensité de la houle et de l'érosion sur trois plages surveillées pendant la saison de nidification des tortues marines. Les analyses cartographiques montrent une perte totale de nids de tortues luth due à la submersion. Bien que des nids de tortues imbriquées aient également été submergés, l'impact sur la survie des œufs reste à déterminer, car une immersion de courte durée pourrait avoir des effets moins graves, notamment pour les nids situés plus haut sur la plage. Ces observations mettent en évidence les conséquences dévastatrices de l'ouragan Beryl, notamment pour les nids de tortues luth. La fréquence et l'intensité croissantes des ouragans en début de saison pourraient entraîner des conséquences à long terme sur les populations de tortues marines des Caraïbes.

Mots-clés : Tortue marine; Martinique; *Dermochelys coriacea*; *Eretmochelys imbricata*; Ouragan; Nidification; Érosion.

Cette note intitulée « *Early-Season Hurricane Beryl's Impact on Marine Turtle Nesting in Martinique* », a été publiée dans sa version finale en 2024 dans la revue *Caribbean Journal of Science*. En tant que première auteure, j'ai proposé l'idée originale, réalisé l'essentiel de la recherche sur l'état de la question, mené les analyses cartographiques et assuré la rédaction principale du manuscrit en partenariat avec Chloé Vanleynseele qui a contribué aux analyses cartographiques et à la rédaction. Les professeurs Benjamin de Montgolfier, Dennis Fournier et Réjean Tremblay ont supervisé la révision de l'article. Les professeurs Benjamin de Montgolfier, Dennis Fournier et Réjean Tremblay, ainsi que le chercheur Erwann Fraboulet ont permis l'acquisition des fonds. Une version enrichie de l'article, incluant des données supplémentaires relatives à l'ouragan Elsa et à la tempête Bret, a fait l'objet d'une publication dans la revue *Le Climatoscope* en 2025.

EARLY-SEASON HURRICANE BERYL'S IMPACT ON MARINE TURTLE NESTING IN MARTINIQUE

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1.2 ABSTRACT

The countries of the Caribbean basin are regularly subjected to intense climatic events such as hurricanes. In early July 2024, Hurricane Beryl became the earliest Category 4 hurricane on record, striking Martinique with unprecedented intensity. These extreme weather events pose a significant threat to the breeding success of endangered sea turtles in the Caribbean. The main objective of this research was to determine the direct impact of Hurricane Beryl on the nesting populations of leatherback turtles (*Dermochelys coriacea*) and hawksbill turtles (*Eretmochelys imbricata*). We estimated the different levels of the coastline in order to evaluate the evolution of the sea level height, swell intensity, and erosion across three beaches that were being monitored during the sea turtle nesting season. Map analyses show a total loss of leatherback turtle nests due to submersion. While hawksbill turtle nests were also submerged, the impact on egg survival is yet to be fully determined as short-term immersion could have less severe effects, especially for nests located further from the shoreline. These observations highlight the devastating consequences of Hurricane Beryl, in particular for leatherback turtle nests. The increasing frequency and intensity of early-season hurricanes may have long-term implications for sea turtle populations in the Caribbean.

Keywords: Sea turtle, Martinique, *Dermochelys coriacea*, *Eretmochelys imbricata*, Hurricane, Nesting, Erosion.

1.3 INTRODUCTION

On July 1st, 2024, Hurricane Beryl, a Category 4 storm on the Saffir-Simpson scale, made landfall in the Lesser Antilles, marking the earliest major hurricane of the Atlantic season since hurricane Dennis in 2005 (Météo France, 2024). Berryl's rapid intensification, evolving from a tropical depression to a major hurricane in just 42 hours, is unprecedented for this time of year. This makes Beryl a remarkable climatic anomaly to study. On July 1st, 2024, Beryl's eye reached the Archipelago of St. Vincent and the Grenadines, located 200 km south of Martinique, where this study takes place (NOAA, 2024). In Martinique, Beryl generated sustained winds of 70 to 100 kph, with a maximum of 122 kph on the North Caribbean coast (Météo France, 2024). Beryl also caused a significant rise in sea levels, with waves reaching heights of four to five meters (Météo France, 2024), causing important coastal submersion. Long and short-term ecosystem modification was observed by hurricanes due to their high intensities and frequencies (Scatena & Larsen, 1991). They have a fundamental role in the coastal region's ecology, which are key nesting areas for many migratory species, including sea turtles (Dewald et al., 2024).

Different turtle species can be found with their nesting periods naturally overlapping the hurricane season (Hirth, 1980; Milton et al., 1994; Chevalier & Lartiges, 2001; Price et al. 2004). Hurricanes can drastically affect reproductive success through mechanisms such as rising sea levels, drowning incubating embryos and eroding nests (Dewald et al., 2014; Pike et al., 2015). Future laying may also be disrupted by debris washed up by the sea (Fujisaki et al., 2016). Habitat modifications, such as the shortening or disappearance of sand beaches and the destruction of mangroves and other vegetation, can affect the rest of the nesting season (Long et al., 2011). The incubation period, which averages 60 days (Chevalier & Lartiges, 2001), is a critical period in the life cycle of sea turtles (Pike et al., 2015). Hurricane Beryl occurred right in the middle of the sea turtle nesting season, during ongoing monitoring by Aquasearch's research office. Aquasearch has been at the initiative of Martinique's sea turtle monitoring since 2020. Martinique's beaches host mainly two species of marine turtles, the leatherback Turtle (*Dermochelys coriacea* (Vandelli, 1761)) and the hawksbill turtle (*Eretmochelys imbricata* (Linnaeus, 1766)), whose nesting periods are respectively from March to July and from mid-April to mid-October (Lescure, 1987). Both species are classified as "threatened" by the IUCN (IUCN, 2020), making them particularly vulnerable to extreme weather conditions. Data collected during the 2024 monitoring season allowed us to record the consequences of Beryl on the nests of these two marine turtle species.

1.4 MATERIALS AND METHODS

This study was carried out on three beaches which gathered a large number of Martinique's sea turtle nests: Madiana beach, located in the Caribbean northwest of the island; Diamant beach located on the southwest on the Caribbean coast; and Salines beach located at the southern tip of the island, where the Caribbean Sea meets the Atlantic Ocean (**Fig. 14**). Madiana has a wide strip of sand with limited vegetation to the south of the beach, while Diamant and Salines have well-developed vegetated backdrop. However, Diamant has a narrow strip of sand.

Figure 14. Martinique, with the location of the three turtle nesting study areas indicated.

From April 1st to October 31st, 2024, different teams conducted monitoring four nights per week to characterize the nesting season of marine turtles in Martinique. The GPS coordinates of every nest (My Tracks v.8.2.0) and the species identification were systematically collected during these monitoring. The coastlines were recorded before the hurricane, the day after and one week after. We used the MyTracks application which records geographic coordinates when walking along the water line. A hypothetical coastline was also reconstructed using people's accounts, data from Météo France and visual evidence using the debris left by the hurricane. In that case, we also walked along the visible marking left on the shore by the submersion while using MyTracks. All GPS coordinates of the nests as well as the different coastlines were mapped using QGIS software (version 2.7.6), allowing us to determine how many nests were submerged as well as to measure the extent of sea encroachment during Beryl's passage.

1.5 RESULTS & DISCUSSION

From April 1st to June 28th, 2024, we recorded three hawksbill nests in Madiana; 53 nests at Diamant including 41 hawksbills and 12 leatherbacks, and 29 nests at Salines, including 14 hawksbills and 15 leatherbacks. As already shown in the literature, Leather back nests were naturally laid closer to the sea, in sandy environments (Wood & Bjorndal, 2000; Chevalier, 2005). The results of the coastlines make it possible to measure, approximately, the pre- and post-cyclone difference in the height of the sea level. Thus, we find average elevations of 46.5 m in Madiana, 87.7 m in Diamant, and 70.9 m on Salines beach. The latter two were closest to the eye of the hurricane, Beryl. Sea levels, one week after Beryl's passage, remained higher than usual, mainly for the beaches in the south of the island, Diamant and Salines. On Diamant and Salines beaches, all the nests were submerged (**Fig. 15a** and **Fig. 15b**). Floods on these nests can suffocate the eggs through the infiltration of sea water, with the consequences of the asphyxiation varying depending on the duration and frequency of immersion, as well as the stage of development of the eggs (Milton et al., 1994; Foley et al., 2006).

The eggs' viability can be reduced by 10% by a brief flooding of one to three hours, while a more prolonged exposure of six hours could reduce it by up to 30% (Pike et al., 2015). According to Caut, Guirlet et Girondot (2010), the earliest and latest embryonic phases are key moments in the development of turtles, and therefore the most sensitive. In Madiana, two nests appear in the non-flooded area (**Fig. 15c**). However, one was likely submerged as it was no longer accessible due to debris. Indeed, it is important to take into account the sea level, which rose during the passage of the hurricane. In addition, once the hurricane had passed, we observed a significant coastal shrinkage, like in Diamant where only 350 m of sand was left on the west side, a week after the hurricane, and the rest was mainly mangrove falling into the sea (**Fig. 15b**). Salines and Madiana beaches also experienced significant sand strip reductions.

Additionally, numerous fallen coconut trees were observed, consistent with studies showing the sensitivity of old palm trees to strong winds (Zimmerman et al., 1994; Duryea et al., 1996; Zimmerman & Covich, 2007; Lugo & Frangi, 2016). It is particularly observed that there is a loss of habitat on the east side of Madiana defined by the disappearance of a part of the forest (**Fig. 15a**). It would be preferable to favour tree species with large bulbs, with a well-anchored root system as well as a slow growing trunk, and therefore relatively powerful and resistant to strong gusts of wind (Marty et al., 1986). Large quantity of eggs was found littering the beaches, mixed with sargassum washed up during the hurricane. The submersion waves resulting from the hurricane completely flooded the beaches, and therefore the nests. Sea turtle eggs being permeable, this is allowing the exchange of gas and water with the external environment, but it is also making them drown during immersion. The waves caused by this extreme weather can therefore limit both the number of nests on the beach, through drowning, burial and/or erosion, but also diminish the number of newborns to emerge through drowning of the embryos (Ackerman, 1997).

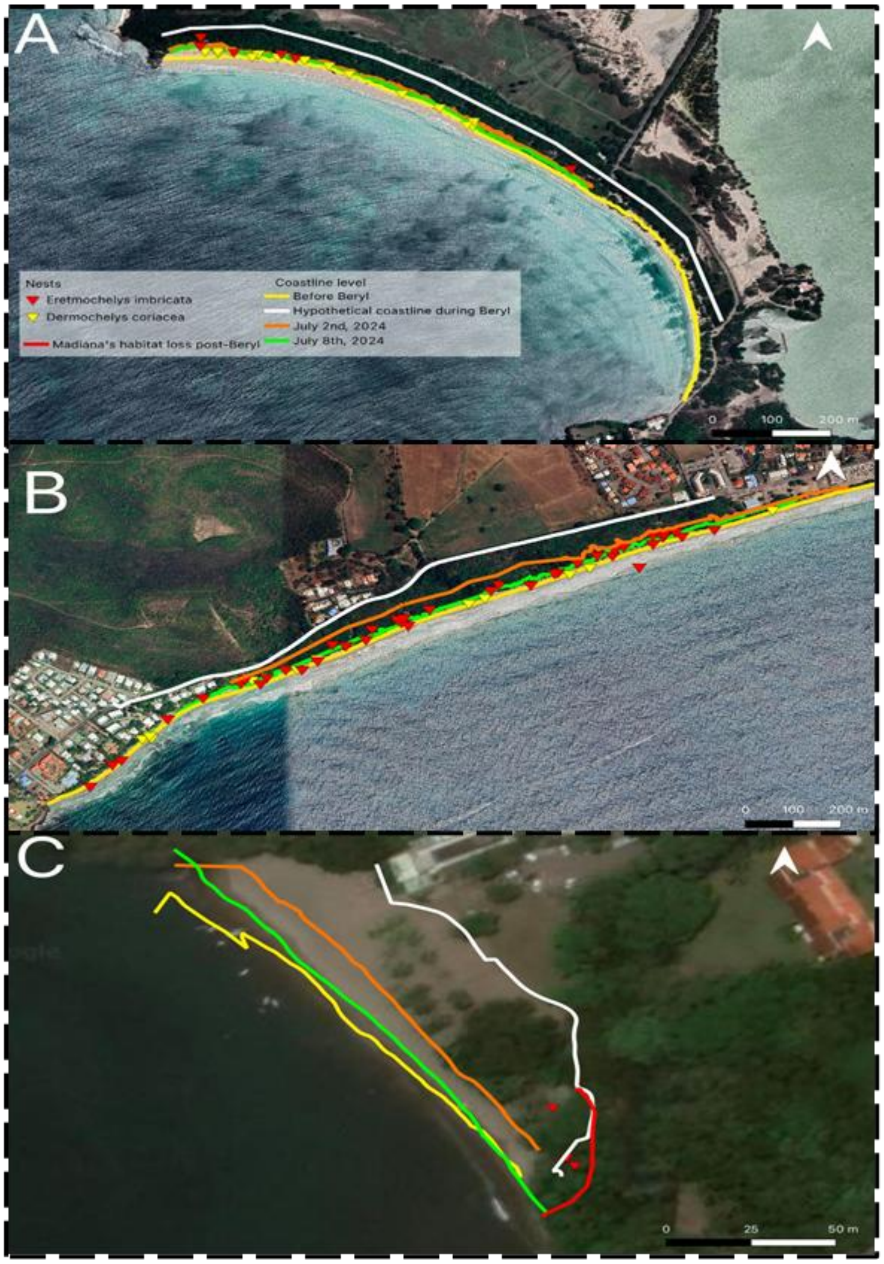

Figure 15. Maps of the three studied beach. (a) Salines; (b) Diamant; and (c) Madiana where the nests' location were indicated by red triangle for hawksbills (*Eretmochelys imbricata*) and yellow triangles for leatherbacks (*Dermochelys coriacea*). Different sea coastlines level are indicated through lines: before Hurricane Beryl (yellow); during Hurricane Beryl (white); the day after (orange); and a week after (green). Another line (red) in (c) shows the forest area that has disappeared after the hurricane.

Given the incubation period of 60 days, nests laid after May 2nd, 2024, were either washed away by waves or flooded, which results in the death of the embryos and a zero-emergence rate can be expected. This represents three hawksbill nests in Madiana, 47 nests in Diamant (including eight leatherbacks), and 26 nests at Salines (including 13 leatherbacks). Leatherback turtles, which tend to nest closer to the water, lost 84% of the season's nests, as their proximity to the waterline increases the risk of nest erosion, despite their depth, which varies from 60 to 90 cm (Wood & Bjorndal, 2000).

The leatherbacks' unimpacted nests had simply hatched before the arrival of the hurricane. As for the hawksbill turtles, during the pre-hurricane period, 94.5% of nests were lost, given that the nesting season of this species begins later in the season (Chevalier & Lartiges, 2001). The later-laying females might mitigate these losses if no further hurricanes strike the island. However, because hawksbill turtles generally lay their eggs higher up in the vegetation, it could have saved some eggs from drowning, even if the shallow depth of their nests, which is generally between 45 and 70 cm, also exposes them to erosion, particularly during storms (Bossuyt, 2024). The early occurrence of hurricane Beryl did not have the same impact on the different species of turtles. In fact, the nesting season for leatherback turtles was over during the hurricane, meaning that females will not return to lay eggs on the beaches this year.

Hurricane Dean, which hit Martinique on August 16, 2007, is an obvious example of the environmental impact on these species. Leatherback and hawksbill turtle's nests were seriously damaged during Dean (Cayol et al., 2008), similar to the impact observed during more recent storms Elsa (2012) and Bret (2023) (Bossuyt, 2024). GPS records had already revealed a significant decrease in beach width at the western end of Salines beach during Bret as well as damage to Diamant beach, with a subsidence of approximately 0.25 m and a reduction in the width of the beach of 5 m (Bossuyt, 2024), as we observed this year during the hurricane Beryl. Measurements taken by Bossuyt (2024), a month after Bret's storm showed that the humidity was 100% at 75 cm deep till the vegetation edge, which created critical conditions that restricted the essential gas exchanges for the survival of the eggs

(Bossuyt, 2024). Climate change has major consequences on the reproduction of sea turtles, such as rising ocean levels eroding beaches, reducing available nesting sites, and increasing competition for favourable areas (Fish et al., 2005). In addition, extreme phenomena such as Beryl will become more frequent, placing greater pressure on these endangered species, particularly for the leatherback turtles whose preferred sandy areas are likely to disappear first (Pike & Stiner, 2007; Dewald et al., 2014; Caderas, 2016). The reproductive strategy of marine turtles, which involves laying numerous eggs in different places on the beach, at intervals of weeks and in seasons spaced two to five years apart, may help balance losses like those experienced during hurricane Beryl (Ackerman, 1997). Finally, we can notice that no post-hurricane decrease in egg-laying activity was noted, the number of observations remained stable, and egg-laying was observed the day after the hurricane.

1.6 CONCLUSION

Statistically, high category hurricanes typically occur between mid-August and late September. However, the warm sea surface temperatures observed in the North Atlantic, comparable to those usually seen in late August, explain the precocity of Beryl (Météo France, 2024). While the overlap of hurricane and sea turtle nesting season is common in the Caribbean, hurricanes usually arrive at the end of the nesting season, minimizing their devastating impact. Yet, Beryl having arrived very early in the season potentially has a greater impact on the progress of the nesting season and on the renewal of the sea turtle population. Hurricanes can have long-term effects, as it can take up to several years for a beach to return to normal (Spiske et al., 2022; Engelbrecht, 2024). Indeed, the beach and forest reformation are long processes and extremely dependent on climatic hazards. According to Jn Baptiste (2021), solutions for beach stabilization exist, such as revegetation or the use of vegetated gabion baskets. In addition to their ecological importance, sandy beaches are a significant element in the economy of many Caribbean islands because they attract a large number of tourists (Spencer et al., 2022), which is why habitat restoration seems to be a sustainable solution to limit coastal erosion and preserve nesting sites.

CHAPITRE 2

DYNAMIQUE DE NIDIFICATION DES TORTUES IMBRIQUÉE ET LUTH : QUATRE ANS DE PHOTO-IDENTIFICATION EN MARTINIQUE

2.1 RESUMÉ

L'une des principales limites des études de conservation réside dans l'estimation précise de la taille des populations afin d'adapter les mesures de gestion. Il est donc essentiel d'éviter les doublons de comptages individuels afin d'éviter toute surestimation de la taille des populations. La photo-identification (photoID) offre une alternative peu coûteuse et non invasive pour le suivi des animaux migrateurs, mais elle reste généralement sous-utilisée chez les espèces marines. Dans cette étude, nous avons appliqué pour la première fois la photoID aux populations de tortues marines des Antilles françaises, contribuant ainsi aux efforts mondiaux de recensement des populations dans les Caraïbes tout en minimisant le stress et les dommages causés aux tortues. Nous nous sommes concentrés sur deux espèces préoccupantes, *Dermochelys coriacea* (la tortue luth) et *Eretmochelys imbricata* (la tortue imbriquée), identifiées grâce à une méthode de reconnaissance semi-automatisée afin d'analyser leur comportement de nidification. Notre suivi pluriannuel a nécessité 5 292 heures de surveillance nocturne sur trois plages de la Martinique pendant quatre ans, fournissant des données précieuses sur les comportements de nidification, la dynamique des populations et les besoins de conservation. Nous avons recensé 57 observations de tortues luth, avec un taux de recapture de 61%, et 314 observations de tortues imbriquées, avec un taux de recapture de 36%. Le microhabitat de chaque nid a été enregistré, fournissant des informations sur les préférences des sites de nidification. De plus, les tortues luth présentaient un intervalle de temps plus long entre leurs différentes heures d'arrivée sur la plage contrairement aux tortues imbriquées. Ces résultats révèlent des différences comportementales significatives et des habitudes de nidification spécifiques, soulignant le potentiel de l'expansion de la photoID, combinée à l'analyse écologique, comme ressource précieuse pour la gestion de la conservation des espèces de tortues marines menacées.

Mots-clés : En danger, Tortue marine, Martinique, *Dermochelys coriacea*, *Eretmochelys imbricata*, Photo-identification, Microhabitats, Comportement.

Cet article, intitulé « Nesting dynamics of hawksbill and leatherback turtles: a four-year photo-identification study in martinique », a été publié dans sa version finale en 2025 dans la revue *Journal for Nature Conservation*. En tant que première auteure, j'ai réalisé l'essentiel de la recherche sur l'état de la question, mené les analyses et le travail de terrain, assuré la rédaction principale du manuscrit. Vittoria Calabretta et Céline Valin ont aidé au traitement et à la gestion des bases de données photos. Le professeur Benjamin de Montgolfier a fourni l'idée originale. Les professeurs Benjamin de Montgolfier, El Mahdi Bendif et Réjean Tremblay ont supervisé l'étude et participé à la rédaction. Les professeurs Benjamin de Montgolfier et Réjean Tremblay, ainsi que le chercheur Erwann Fraboulet ont permis l'acquisition des fonds. Une partie de ces travaux a été présentée à la conférence Aquaecomics 2025 à Evian (France).

NESTING DYNAMICS OF HAWKSBILL AND LEATHERBACK TURTLES : A FOUR-YEAR PHOTO IDENTIFICATION STUDY IN MARTINIQUE

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2.2 ABSTRACT

One major limitation in conservation studies is accurately estimating population size to adapt management efforts. Thus, avoiding individual duplicate counts is essential to prevent any overestimation of population size. Photo-identification (photoID) offers a low cost and non-invasive alternative for monitoring migratory animals, and yet, it remains generally under-implemented in marine species. In this study, we applied photoID with sea-turtle populations in the French Antilles for the first time, thereby contributing to global population survey efforts in the Caribbean while minimising stress or harm to turtles. We focussed on two species of concern, *Dermochelys coriacea* (leatherback) and *Eretmochelys imbricata* (hawksbill), identified through a semi-automated recognition method to analyse their nesting behaviour. Our multi-annual survey involved 5 292 hours of night monitoring across three Martinique beaches over four years, yielding valuable data on nesting behaviours, population dynamics and conservation needs. We recorded 57 occurrences of leatherback turtles with a recapture rate of 61%, and 314 hawkbill observations with a recapture rate of 36%. The microhabitat of each nest was recorded, providing insights on nesting site preferences. Additionally, leatherbacks exhibited a longer time interval between their arrival on the beach and the start of nesting activity compared to hawksbills. These results reveal significant behavioural differences and specific nesting habits underscoring the potential of expanding photoID combined with ecological analysis, as a valuable resource for conservation management of threatened sea-turtle species.

Keywords: Endangered, Sea turtle, Martinique, *Dermochelys coriacea*, *Eretmochelys imbricata*, Photo-identification, Microhabitats, Behaviour.

2.3 INTRODUCTION

Accurately estimating population size is a critical challenge in conservation studies, as it directly informs adaptive management strategies and necessitates meticulous methods to avoid duplicate counts and consequent overestimations. In response, emerging technological advances—especially in image analysis and photo-identification (photoID)—are revolutionizing the field, enabling researchers to overcome these traditional hurdles and implement large-scale monitoring of animal populations, with notable promise for studying migratory species (Wursig & Wursig, 1977; McDonald & Dutton, 1996; Wilson & McMahon, 2006; Holmberg et al., 2009). As such, individually identifying animals through naturally occurring markers has become a cornerstone of conservation research (Whitehead et al., 2000; Frisch & Hobbs, 2007) and these non-invasive approaches are now becoming central to capture-mark-recapture studies (Rosel et al., 2011; Dunbar et al., 2021). This shift offers a less intrusive, low cost, and sustainable alternative to traditional marking techniques (Araujo et al., 2016). Conventional methods, such as physical tagging-often leading to significant tag loss (Bradshaw et al., 2000; Reisser et al., 2008)- or the use of microchips, which requires expensive, specialized equipment, and impose stress on animals (Buonantony et al., 2008; Gheorghiu et al., 2010), underscore the urgency of adopting improved strategies in population monitoring of endangered species. In contrast, photoID offers a simpler, more portable, and accessible approach that can be used by researchers and citizen scientists alike, making it a valuable tool in modern conservation efforts (Schofield et al., 2008).

Located in the Caribbean, more specifically, in the Lesser Antilles, Martinique is an Island covering 1 128 km, recognized as a biodiversity hotspot where its endemic species are facing significant threats due to human activities and climate change (Myers et al., 2000; Anadon-Irizarry et al., 2012; Hrdina & Romportl, 2017). For marine turtles, Martinique plays a key role in their development (Chevalier, 2006; Cayol, Maillard & Dubief, 2008). Each year, from April to October, this island hosts numerous nesting sites for hawksbill (*Eretmochelys imbricata* (Linnaeus, 1766) and leatherback turtles (*Dermochelys coriacea* (Vandelli, 1761)) (Chevalier, 2006; Dow et al., 2007). Moreover, these two species highly represented in Martinique are classified as “critically endangered” and “vulnerable” respectively (IUCN, 2020), placing the island at the fore front of species restoration programs.

Amongst marine turtle, the leatherback turtle is the largest species and the sole representative of the Dermochelyidae family. It can reach up to 2 m in length and weigh more than 900 kg (Eckert & Luginbuhl, 1988). In the Atlantic Ocean, females generally return every 2 to 5 years to nest on tropical and subtropical beaches (Bell et al., 2004; James et al., 2007) before heading back to their feeding areas, which are mostly located in temperate waters (Dodge et al., 2014). During a single nesting season, females may nest up to 11 times (Rostal et al., 1996; Bell et al., 2004) with intervals of 8 to 12 days between nestings (Eckert et al., 1989; Buonantony et al., 2008). Unlike any other sea turtles, leatherback turtle has a unique shell composed of a hard dermal tissue rather than scales. Because traditional photoID methods of sea turtles have relied on facial scales, applying them to leatherback turtles has proven unworkable due their unique lack of scales. However, McDonald and Dutton (1996) suggested using the pineal spot also called “pink spot”- a depigmented mark located on the top of the head. Subsequent research (Buonantony et al., 2008) has demonstrated that this mark persists over time and is efficiency for population study using photoID, allowing reliable individual identification of leatherback turtles (Pauwels et al., 2008; De Zeeuw et al., 2010). Moreover, the pineal spot can be used for individuals encountered in the open sea, enabling comparisons with those photographed in nesting areas (Buonantony et al., 2008).

The hawksbill turtle measures about 90 cm in length (Pritchard & Mortimer, 1999) and nests on subtropical and tropical beaches up to nine times during the nesting season, with intervals of 9 to 21 days between nestings (Limpus et al., 1983; Bjorndal et al., 1985). Females would come back every 1 to 6 years, with an average of 2 years (Richardson et al., 1999; Beggs et al., 2007). Like other members of the Chelonian family, the hawksbill can be identified by its unique scutes pattern. Indeed, scute colouration and morphology are recognized as reliable markers for individual identification, whether using facial patterns (Reisser et al., 2008, Calmanovici et al., 2018; Dunbar, Hudgins & Jean, 2021), flippers

(Gatto et al., 2018; Pursley, 2020), or the shell (Tabuki et al., 2021). Facial scutes are particularly valuable because they remain very stable and unique, allowing for consistent identification over time (Dunbar et al., 2014). Research has shown that the scute pattern remains unchanged in hawksbill turtles for at least 3 years (Carpentier et al., 2016).

The threatened status of hawksbill and leatherback turtles is attributed to several factors, including habitat loss (Mazaris et al., 2009; Witherington et al., 2011), climate change (Fuentes et al., 2019; Topping & Valenzuela, 2021), and anthropogenic pressures (Sella & Fuentes, 2019, Stanley et al., 2020; Siqueira-Silva et al., 2020). Estimating individual identification for understanding nesting site preference and site fidelity is vital for assessing nesting success (Richardson et al., 1999; Hays, 2000). Although, counting nesting turtles has long been considered a reliable method (Sims et al., 2008; National Research Council et al., 2010; Santos et al., 2021), this approach can be inaccurate because the same individual may nest several times in one season (Esteban et al., 2017). Based on satellite tracking of green turtles, Esteban, Mortimer and Hays (2017) demonstrated that traditional nest counts may substantially overestimate nesting success, by nearly a factor of two, due to repeated nesting by the same individuals. This finding highlights the limitations of relying solely on nest counts without incorporating individual identification, a bias that likely extends to other species such as hawksbill and leatherback turtles. Although we recognize that photo- identification cannot fully resolve this issue when beaches are not monitored daily, it nonetheless represents a valuable approach for enhancing the accuracy of nesting estimates, particularly in contexts where continuous or extensive monitoring is not feasible. To date, however, similar high-resolution tracking studies aimed at quantifying this overestimation remain scarce or absent across the Caribbean. Although some local monitoring programs have recognized intra- seasonal remigration (Maurer et al., 2022), few provide adjusted nesting estimates that account for this phenomenon. This gap highlights the need to integrate complementary approaches, such as photoID, into annual sea turtle monitoring efforts to improve demographic assessments.

PhotoID offers here an adequate and accurate alternative by preventing duplicate counts, as it distinguishes individuals through their unique patterns, thereby yielding more reliable data to inform conservation strategies (Schofield et al., 2008). Moreover, photoID data can be integrated with other information gathered during the nesting seasons (e.g., female body size, number of eggs laid, nest location, and habitat characteristics) to enrich our understanding of local populations (Kamel & Mrosovsky, 2005; Gaos et al., 2021). On a larger scale, photoID monitoring can be applied to track individual migrations and estimate migratory routes, making it an effective conservation tool for marine turtles' survival.

In this context, our study was oriented towards several objectives: (1) to collect data on female leatherback and hawksbill turtles nesting on three beaches in Martinique, monitored over a four-year period, (2) to determine intra-annual and interannual "recapture" (remigration) rates using photoID, and (3) to analyse nesting habits and site fidelity, microhabitat selection, and temporal patterns. This study is based on the assumption that photoID is a non-invasive method that reduces bias in population estimates and aids in evaluating interspecific differences in nesting behaviour.

2.4 MATERIAL AND METHODS

2.4.1 Study Sites

This study is based on the population of leatherback and hawksbill turtles nesting on three beaches in Martinique: Madiana, Diamant, and Salines (**Fig. 16**). Madiana and Diamant beaches are located on the Caribbean coast while Salines is situated along the island's Atlantic south coast (**Table 1**).

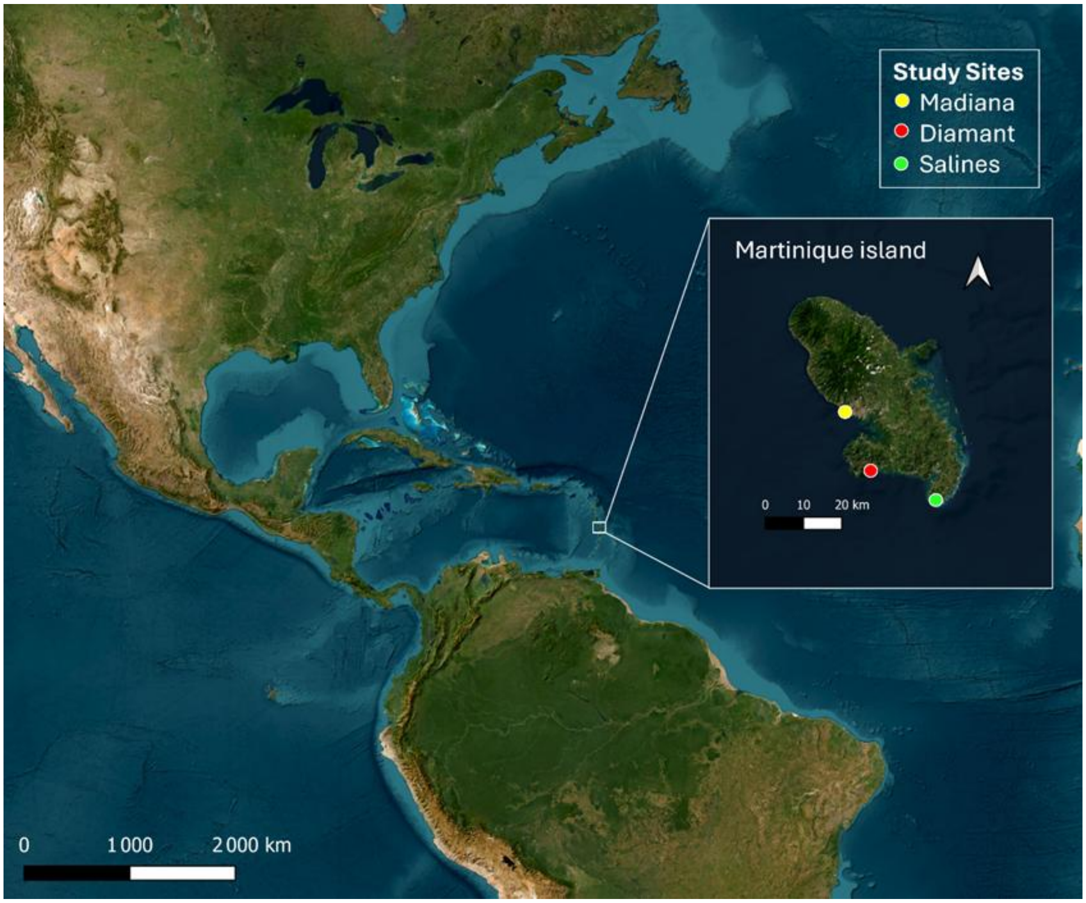

Figure 16. Location of the three monitored beaches on Martinique Island, Lesser Antilles.

Table 1 Characterisation of the three studied beaches.

Beach name	Coordinates		Length (km)	Characteristics	Closest town
Madiana	14°36'43"N	61°05'54"W	0.2	Black sand	Schoelcher
Diamant	14°28'32"N	61°02'10"W	2.3	Mix white/black sand	Diamant
Salines	14°24'14"N	60°52'47"W	1.3	Fine white sand	Sainte-Anne

2.4.2 Data Collection

Sampling was conducted from 2020 to 2024, four nights per week (Monday/Tuesday and Thursday/Friday) between 7:00 p.m. and 1:00 a.m. The duration of the sampling period varied by year, ranging from a minimum of July to September in 2020, to a maximum of April to October in 2023 (**Table 2**). In 2021 the monitoring stopped in July due to the Covid-19 restrictions in place. This study represents a sampling effort of 5 292 h, or 1 764 h per monitored beach. A total of 815 hawksbill turtles and 105 leatherback turtles were observed or reported (tracks included) during the 4 years nesting season night patrols.

Table 2. Sampling effort per beaches and years of monitoring.

Year	Sampling period	Total Monitoring (h)	Madiana	Diamant	Salines
2020	July-September	540	180	180	180
2021	April-July	1254	418	418	418
2023	April-October	1782	594	594	594
2024	April-September	1716	572	572	572

Teams of at least four students, trained by Aquasearch, conducted their patrols under red light. Each pair within a team began at opposite ends of the beach and moved toward the centre, where they paused for a 20-minute break before continuing. This method ensured comprehensive coverage of the beach. Due to its small size (200 m), only Madiana Beach was patrolled by a single pair of students. All collected data and photographs were taken during the laying phase, minimising the impact of data collection on the nesting behaviour of the turtles. Experimental procedures were evaluated and approved by the Ethical-Scientific Committee for Animal Experimentation of the Université du Québec à Rimouski (Certificate Number CPA-97-23-261).

Collected data included the arrival and return times of turtles that came to lay eggs, number of eggs laid, width of the turtles' tracks, GPS position of the nests, and their habitats. Track width refers to the measurement (in cm) of the marks left in the sand by the turtle's front flippers. It is taken at the widest point of the flipper imprints using a flexible tape measure. Egg count error indicates the observer's estimated margin of error when the clutch had already been laid. This study specifically identifies various habitat types and associated microhabitats, as detailed below. Morphometric features of the observed turtles were also recorded by measuring the Curved Carapace Length (CCL) and Curved Carapace Width (CCW) using laser in order to not touch the animal. We used the Long Range Tactical Red SVIP Gift Positioner laser system (red laser pointers, Accessories Energie, Nice, France), mounted on the end of a calibrated bracket with two laser beams fixed precisely 30 cm apart. This configuration ensured consistent projection of a 30 cm reference scale. Calibration tests were per formed at multiple distances to verify the stability of the spacing. Turtle measurements were obtained by photographing the laser dots projected onto the carapace and estimating carapace dimensions using MESURIM Pro software (Académie de Créteil, France). Photographs were taken with a typical cell phone, as all contributors would have their own. Photographs were taken under red light without flash, at a distance around one metre from the turtle. For the right and left profiles of the head, images were captured horizontally at eye level. The dorsal view of the head was photographed from a height of about one metre directly above the turtle. For leatherbacks, only the top of the head, specifically the area containing the distinctive "pink spot", was used for identification. In contrast, for hawksbills, both the right and left sides of the head were considered. Pictures were then systematically catalogued each day, with specific information of each individual turtle associated to each picture file. Turtles returning to the water having only made a nesting attempt or a simple search for future laying grounds were also photographed. However, to minimise any disturbance, photographs were only taken right before the female entered the water.

2.4.3 PhotoID

In order to analyse the pictures, we used the software I3S Pattern v3.0 (Interactive Individual Identification System, © 2020 Reijns/i3s) that allowed a semi-automated recognition of individual turtle. This software is largely used in literature for its effectiveness and reliability (Speed et al., 2007; Van Tienhoven et al., 2007; Den Hartog & Reijns, 2012; Steinmetz et al., 2018). Based on photo quality (Dunbar et al., 2014; Calmanovici et al., 2018) and user experience (Steinmetz et al., 2018), I3S Pattern is recognized as a reliable semiautomatic tool. Although photoID has proven effective for monitoring individual sea turtles (McDonald & Dutton, 1996; Buonantony et al., 2008; Esteban et al., 2017), its reliability is challenged by several factors. Image quality remains a major limitation; suboptimal lighting, motion blur, and inconsistent angles can significantly impair the performance of auto mated recognition software (Calmanovici et al., 2018). These issues become even more pronounced as database size grows, making manual verification of proposed matches increasingly time-consuming yet still essential (Dunbar et al., 2014). To address these challenges, we standardized our photo collection protocols—ensuring consistent capture angles, among other measures. In this study, three anchor points were used to guide the software and outline the studied area, here, the top head of the leatherback and scales on the right or left profile of the hawksbill. Once the studied area was established, the software, I3S pattern, will automatically designate 35 key reference points (Den Hartog & Reijns, 2014) for size and location comparison in each image of the database. The software will then suggest matches by assigning them a score. Scores between 0 and 20 typically reflect a high likelihood of accurate identity matching, whereas higher values indicate a substantially lower probability of true correspondence. Despite this, users were encouraged to visually assess the top-ranked image suggestions regardless of score. Final verification of each match was conducted manually to ensure data integrity. To reduce observer bias, the same individual reviewed all data twice, followed by an independent check by a second reviewer. These methodological refinements reinforce the validity of photoID as a reliable, non-invasive tool for recognizing in dividual sea turtles in conservation efforts.

2.4.4 Habitat Characterization

We identified four primary habitat types. The first is the waterline, extending up to 20 m from the low tide mark. The second is the sand strip, whose width varies depending on the beach, for instance, Madiana is characterized by an expansive sandy area with minimal vegetation. The remaining two habitats are the forest edge and the forest interior. The forest edge is defined as the transitional zone encompassing the final two metres of the sand strip and the initial two metres of the forest, typically influenced by partial shading from the canopy. Beyond this lies the forest interior, which is generally dense and markedly darker due to the overhead vegetation. In spring 2023, we characterized microhabitats at Madiana and Diamant, followed by Salines in 2024, using the Braun-Blanquet method to ensure a systematic and standardised approach (Meddour, 2011; Lemercier, 2023). This method allowed us to define microhabitats based on distinct plant species compositions and abundance level.

Through this process, we identified three vegetation types: ground cover, short shrub and tall shrub. Vegetation cover density for each habitat type was evaluated using the Braun-Blanquet phytosociological method (Westhoff et al., 1978; Meddour, 2011; Lemercier, 2023). To randomly determine the lower left corner of each sampling quadrat, a stone was thrown within the microhabitat. Vegetation cover was then visually estimated using the semi-quantitative Braun-Blanquet abundance-dominance scale, based on the proportion of ground covered by vegetation—including ground-level, shrubby, and arboreal species—relative to bare surface area. In treeless microhabitats, 1 m × 1 m quadrats were used, whereas 2 m × 2 m quadrats were applied in areas containing trees. To ensure data reliability and capture spatial variability, five replicates were carried out per microhabitat. To minimise observer bias and ensure consistency, all characterisations were per formed by a single observer on each beach. Identified microhabitats are available in Annexe I (see supplementary data online at https://doi. org/10.1016/j.jnc.2025.127124).

2.4.5 Data Analysis

All statistical analysis were carried out using R Statistical Software (V.4.2.1; R Core Team 2022) and Microsoft Excel. PhotoID results were compared with the habitat data as well as the monitoring collected in formation (turtle's size, nest coordinates, behaviour). Descriptive statistics (mean ± SD) were used to summarize morphological traits and clutch data. Inter-species differences in time intervals on the beach of each female were assessed using Welch's t-test. Beach potential preference was tested by one-way ANOVAs tested for variation in the number of hawksbill and leatherback observations and recaptures across different beaches. When assumptions of normality or homoscedasticity were violated, Kruskal-Wallis tests were applied. To account for spatial variability, data were normalized per 100 m of beach length and compared using t-tests. Nest site fidelity was investigated by individual identification through photoID and GPS coordinates of nests across habitat types and microhabitats were analysed and interpreted descriptively. To assess the spatial distribution of nesting activity, we employed QGIS spatial tools to calculate the nesting area of individual hawksbill turtles. For each female that nested at least three times during the season and for whom GPS coordinates of nest locations were available (n = 14), we generated a polygon encompassing all recorded nest sites. The resulting polygons represent the spatial extent of each turtle's nesting activity (in m^2). These values were subsequently used to examine the relationship between turtle size, measured as curved carapace length (CCL), and nesting area.

2.4.6 Data Privacy and Ethical Considerations

To safeguard sensitive ecological data, such as nesting site locations and individual turtle identifications, all GPS coordinates and photoID images are stored on secure, access-restricted servers managed by Aquasearch. Access is granted solely to authorized researchers directly involved in the project. Given the potential risk of nesting site exploitation—particularly concerning endangered species like hawksbill and leatherback turtles—precise location data are not made publicly available. However, these data may be shared with qualified researchers upon request to Aquasearch, pending approval.

2.5 RESULTS

2.5.1 Population Monitoring

A total of 314 hawksbill turtles were photographed over the four- year study period (**Table 3**). Image analysis using I3Spattern software identified 113 matches, representing 45 unique individuals, resulting in a recapture percentage of 36 %. Among these recaptures, three hawks bill turtles were defined as remigrants, indicating that these females returned to nest on the same beach across nesting seasons. In contrast, 57 leatherback turtles were photographed during the study period. Image analysis identified 35 matches, representing a recapture rate of 61 %. A closer examination of these 35 pictures using I3S revealed that they corresponded to 11 individuals with multiple intra-annual recaptures. This result suggests a certain degree of fidelity to their nesting sites. It is important to note that no observation of leatherbacks was recorded in 2020, likely due to the late start of monitoring in 2020 that started after the end of the leatherback nesting season in Martinique (March-June). Additionally, leatherback turtles were recorded on only two out of the three monitored beaches (Diamant and Salines).

Table 3. Number of observations (pictures) and recaptures of hawksbill and leatherback turtles on the beaches of Madiana, Diamant, and Salines during the nesting season monitoring of 2020, 2021, 2023, and 2024. Absence of leatherbacks nesting in 2020, could be likely due to the late start of monitoring in 2020 after the end of the leatherback nesting season in Martinique (March-June).

Hawksbill (*E. imbricata*)						
Year	Madiana Observations	Madiana Recaptures	Diamant Observations	Diamant Recaptures	Salines Observations	Salines Recaptures
2020	4	0	21	3	14	0
2021	6	0	36	10	26	15
2023	12	4	52	21	17	4
2024	11	5	65	22	50	29

Leatherback (*D. coriacea*)						
Year	Madiana Observations	Madiana Recaptures	Diamant Observations	Diamant Recaptures	Salines Observations	Salines Recaptures
2020	0	0	0	0	0	0
2021	0	0	3	2	5	3
2023	0	0	2	0	21	13
2024	0	0	11	9	15	8

CCL and CCW measurements were performed on a sample of 281 nesting hawksbill turtles and 86 leatherbacks (**Table 4**; Fig.2 from the supplementary data online at https://doi.org/10.1016/j.jnc.2025.127124). The measurements include all data collected by the monitoring teams, regardless of whether the turtle was seen only once or was recaptured during the season. The average size was 85 ± 6 cm for CCL and 73 ± 7 cm for CCW. Regarding leatherbacks, average CCL size was 157 ± 7 cm, and 110 ± 10 cm in width (CCW). In addition, the average number of eggs laid per nest was 127 ± 10 for hawksbill turtles, compared to 113 ± 10 for leatherbacks.

Table 4. Encountered turtle measurements (CCL and CCW) and track width (in cm) with SD; number of eggs and error during the nesting season monitoring of 2020, 2021, 2023, and 2024.

Hawksbill (*E. imbricata*)					
Year	CCL	CCW	Tracks width	Nb eggs	Error
2020	86 ± 6	74 ± 5	69 ± 12	152	10
2021	86 ± 5	75 ± 4	79 ± 7	127	12
2023	87 ± 5	77 ± 6	72 ± 11	111	10
2024	82 ± 7	65 ± 12	75 ± 8	120	8

Leatherback (*D. coriacea*)					
Year	CCL	CCW	Tracks width	Nb eggs	Error
2020	-	-	-	-	-
2021	149 ± 6	106 ± 10	159 ± 29	123	11
2023	152 ± 8	115 ± 13	178 ± 37	109	11
2024	154 ± 6	109 ± 8	157 ± 26	108	8

Analysis of hawkbill turtles presence per beach using year as replicate revealed that Madiana presents a globally lower values for observations (df: 9, F = 7.28, p = 0.02) and recaptures (Kruskal-Wallis: df: 2, p = 0.12), in particular between Diamant and Madiana which has a significant difference (padj = 0.00411) (Fig. 17a). However, when data were normalized based on the beach length using a standardized 100- meter scale, absence of differences were obtained for observations (t- test: df: 5, F = 1.45, p = 0.31) and recaptures (df: 9, F = 0.46, p = 0.64) results. These last results suggest that hawksbill turtles do not show a clear preference for any of the three beaches (**Fig. 18**). The leatherback turtles were not observed on Madiana beach and their presence in the two other beaches was similar (df: 4, F = 2.62, p = 0.18 for observations and df: 4, F = 0.81, p = 0.41 for recaptures) and lower than hawksbill turtles (**Fig. 17b**).

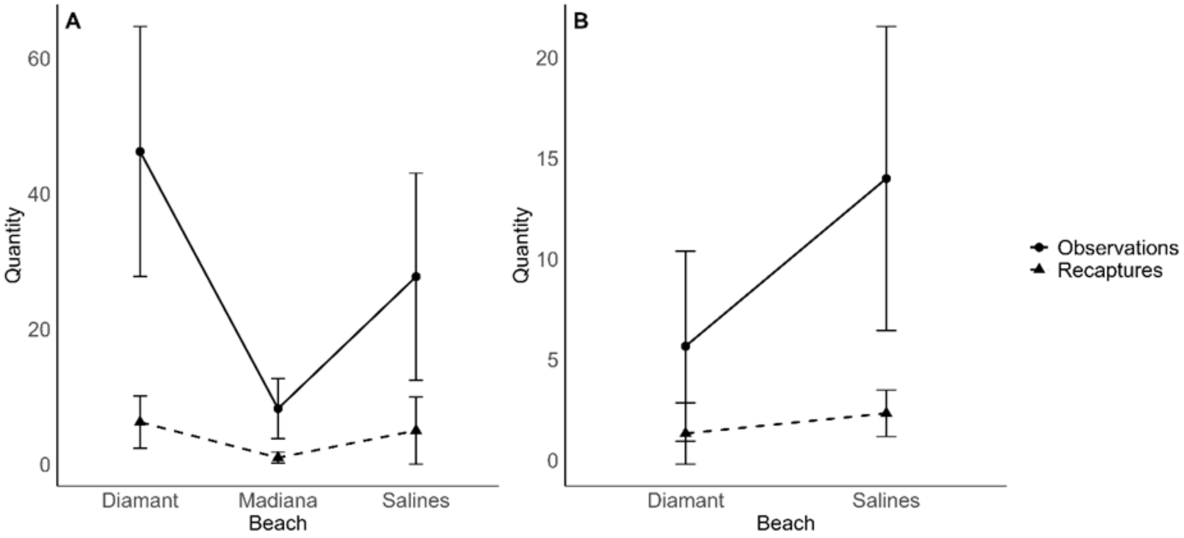

Figure 17. Number of *E. imbricata* (a) and *D. coriacea* (b) observations and recaptures per beach (Madiana, Diamant and Salines). Solid lines represent initial individual observations, while dashed lines indicate photoID-based recaptures.

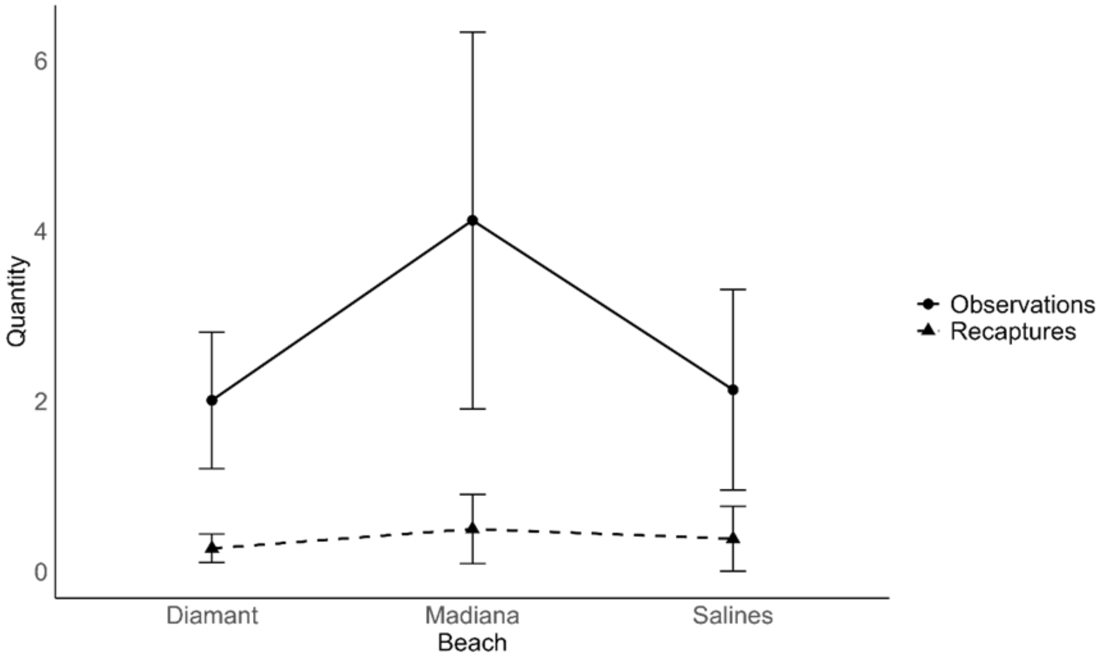

Figure 18. Number of observations and recaptures of E. imbricata turtles per beach and per monitored year normalised on a 100 m beach length. Solid lines represent initial individual observations, while dashed lines indicate photoID-based recaptures.

2.5.2 Nesting Patterns and Beach Arrival Timing

In order to gain insight into the behavioural habits of individual turtles, we focussed on turtles observed more than twice, as identified through photoID using I3S Pattern software. The behavioural analysis focuses on 12 hawksbills and 6 leatherbacks, each observed more than twice—primarily within the same season. However, the small sample size, particularly for leatherbacks, limits the scope for robust statistical analysis. Subsequent analyses were conducted exclusively on these repeatedly observed individuals to elucidate patterns in nesting behaviour and site fidelity. Using QGIS spatial tools, we calculated the area (in m²) encompassing the nest locations of individual turtles. This analysis was conducted for hawksbill turtles that nested at least three times during the season and for which nest coordinates were available ($n = 14$). The resulting polygons represent the spatial extent of each female's nesting activity. On average, hawksbill turtles laid eggs in areas measuring 2 931 m² ± 2 695 m². We aimed to observe how the size of hawksbill turtles (CCL) influences their use of habitat. However, no statistically significant correlation was found ($R^2 = 0.231$; $p = 0.135$). A comparable analysis could not be performed for leatherback turtles due to insufficient data, thereby limiting the scope of our conclusions. When observed, the exact time each female turtle emerged from the water to come ashore was recorded, regardless of whether she ultimately laid eggs. This allowed us to compare time intervals for each species during the nesting season ($n = 6$ for leatherbacks and $n = 12$ for hawksbill). Important individual variability was observed, but on average hawksbill turtles exhibited a shorter water emergence time interval of 1h12min ± 12 min comparatively to 2h48 min ± 24 min for leatherback turtles (**Fig. 19**; t-test = -3.0297, df: 8.23, $p = 0.02$).

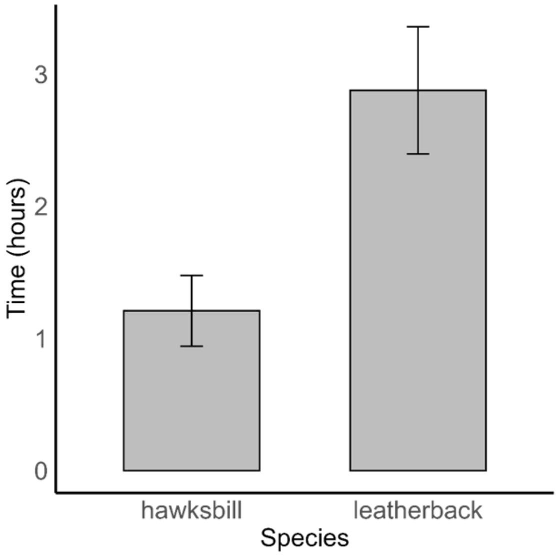

Figure 19. Average time (in hours) between different arrival (water emergence) of hawksbill and leatherback individuals, observed at least 3 times.

2.5.3 Dynamics of Habitat Utilization

We identified nine distinct types of microhabitats (**Fig. 20**) across the three beaches studied, distinct from the four main types of habitats defined previously which are more general (waterline, sand strip, forest edge and forest). Madiana Beach, as a small beach (200 m long), was characterised by low density vegetation predominantly composed of sandy soil (59 %) and high sun exposure. This beach featured sparse populations of coconut trees (*Cocos nucifera*) and seaside grape trees (*Coccoloba uvifera*), classified as Microhabitat M1. In contrast, Diamant Beach exhibited a narrower sand strip (M4 habitat at 62 %) with more diverse vegetation (M5 habitat at 20 %) indicating the dominance of this vegetation structure within this beach. Salines Beach presented a more uniform composition in microhabitats, being primarily dominated by M4 (70 %) characterised by dense arborescent vegetation, and M6 (24 %), which consists of predominantly bushy vegetation.

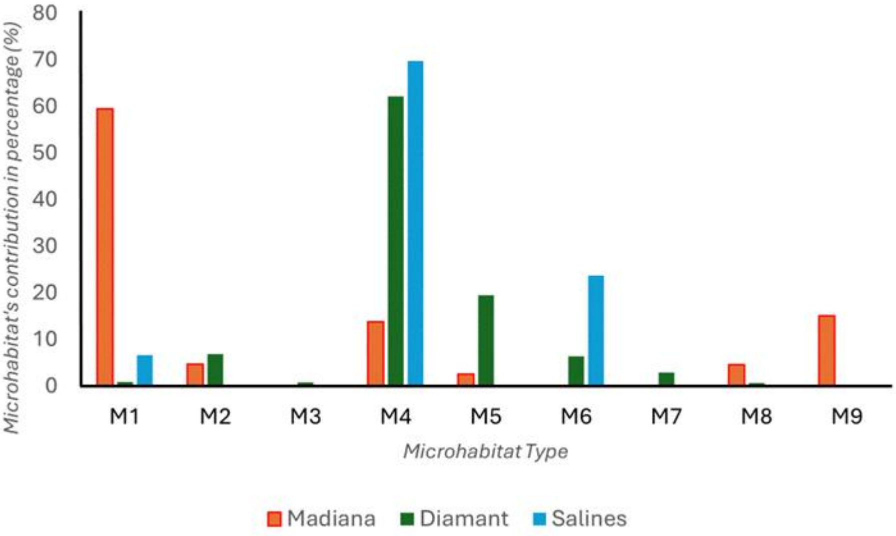

Figure 20. Distribution (in %) of microhabitats (M) by ranges. The floral characteristics of the microhabitats determine their classification. Description available in the supplementary data online at https://doi. org/10.1016/j.jnc.2025.127124.

GPS coordinates of the nests of 100 hawksbill and 29 leatherback turtles identified using photoID indicated that the turtle laid eggs were characterised according to two criteria: the type of habitat (forest, forest edge, sand and waterline) and the microhabitat. Concerning the type of habitat used by the turtles as nesting grounds (**Fig. 21**), hawksbills seem to prioritise the forest unlike the leatherbacks that almost always choose the sand strip and sometimes even the waterline.

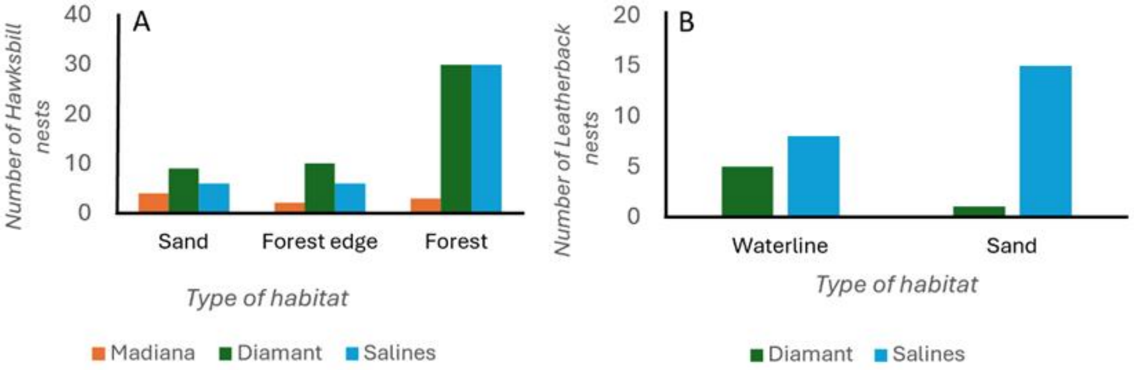

Figure 21. Distribution of clutches across different habitat types (waterline, sand, forest edge, and forest) at Madiana, Diamant, and Salines for: (a) hawksbills (*Eretmochelys imbricata*) and (b) leatherbacks (*Dermochelys coriacea*).

Of the nine microhabitats defined, six of them contained at least one hawksbill nest (**Fig. 22**). However, the totality of leatherback turtle nests were situated directly on the beach sand strip (55 %) or on the waterline (45 %) thus preventing us from classifying these nests into microhabitats. Specifically, on Salines beach, leatherback turtles preferred to lay eggs near the edge of the forest, while avoiding close proximity to it. These nests were located on bare sand areas, sometimes slightly shaded by coconut trees bordering the forest, which prevented the identification of specific microhabitats for leatherbacks. Consequently, the micro habitat analysis focusses on hawksbill turtles. Our observations indicate that 50 % of the nests were laid in microhabitat M4, which is characterized by arborescent vegetation, primarily located in the back forest. M4 is particularly extensive at Diamant and Salines beaches, covering more than 60 % of the surface area (**Fig. 20**), but is considerably smaller at Madiana beach, where it comprises only about 10 % (**Fig. 20**). Microhabitat M6, the second most extensive habitat at Salines (over 20 %), also served as a significant nesting area for hawksbill turtles, accounting for 16 % of the nests recorded at this site. This habitat consists mainly of bushy vegetation interspersed with coconut trees (see Supplementary data at https://doi. org/10.1016/j.jnc.2025.127124). Additionally, a notable proportion (20 %) of hawksbill nests were located in the sand strip area.

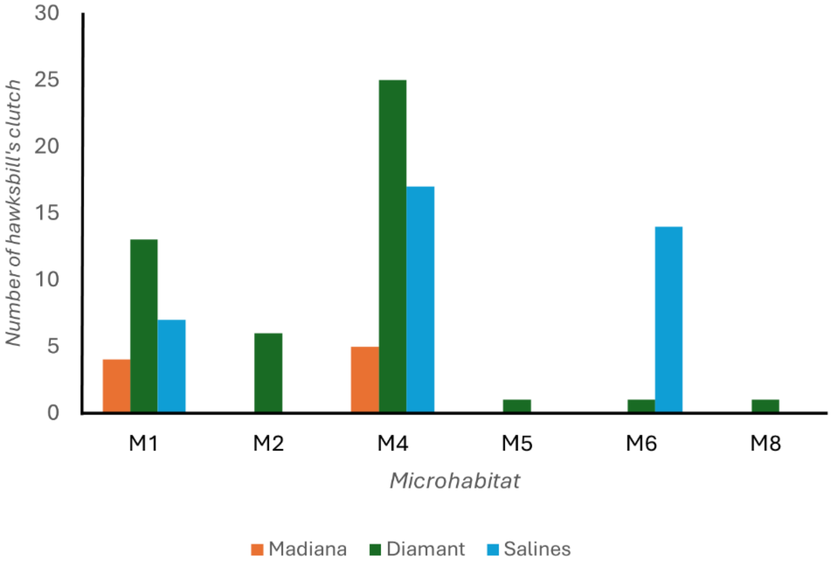

Figure 22. Number of hawksbill's clutches per beaches depending on the microhabitat. The floral characteristics of the microhabitats determine their classification. Description available in the supplementary data online at https://doi. org/10.1016/j.jnc.2025.127124.

2.6 DISCUSSION

This study is the first to report long-term monitoring of hawksbill and leatherback turtle nesting in the French Lesser Antilles, demonstrating the potential of photoID in tracking these populations. The postorbital scales of sea turtles are known for their stability over time (Carpentier et al., 2016), making them an ideal feature for photoID. Hawksbill females recaptured three years after their previous nesting season showed no apparent changes in their head scale patterns. Nevertheless, Carpentier et *al*. (2016) emphasized the importance of further research and continued photoID efforts to monitor potential long-term changes in these patterns. PhotoID technique not only facilitates a more detailed analysis of turtle behaviour during egg-laying but also highlights individual differences, that remain largely unexplored such as specific habitat use or nesting habits. Moreover, tools such as I3S enhance our understanding of sea turtle population dynamics by providing critical data to inform future conservation efforts. Our findings confirm the hypothesis that photoID is an efficient method for assessing population estimates by avoiding duplicate counts and preventing overestimations. With recapture rates of 61 % for leatherback turtles and 36 % for hawkbills, our results underscore the significant risk of overestimating the reproductive effective population if duplicates are not properly identified. For instance, two hawksbill turtles observed in 2020 returned in 2023, and a third individual seen in 2021 reappeared in 2024 (see supplementary data online at https://doi. org/10.1016/j.jnc.2025.127124). This demonstrates site fidelity over multiple years and qualifies them as inter-annual matches. These observations align with the conclusions of Carpentier et al., (2016) and Buteler et al., (2022), demonstrating that photoID is a reliable tool for inter-annual monitoring. While hawksbill nesting habits are well-supported, leatherback interannual patterns and limited data are less thoroughly tied to literature. The absence of returns is attributed to longer remigration intervals (Bell et al., 2004), but additional studies on detection challenges or migration could deepen the interpretation. Moreover, the presence of leatherbacks only reported in Salines and Diamant shows a difference in spatial distribution that may reflect a nesting sites selection due to specific preferences, but this would need further investigations to clarify the ecological factors influencing beach selection by this species.

We also demonstrated that photoID is an efficient tool to infer differences in nesting behaviour between marine turtles' species. Our observations reveal a distinct nesting site preference between the two species studied. Leatherback turtles systematically favour sandy areas close to the water, a behaviour reported by other studies (Whitmore & Dutton, 1985; Kamel & Mrosovsky, 2005). This makes them particularly vulnerable to extreme climatic phenomena. A significant case occurred during our 2024 sampling campaign: Hurricane Beryl struck Martinique on July 1st, at the end of the leatherback turtle nesting period, resulting in the destruction of numerous nests that had not yet emerged. Even in the absence of extreme weather event, nests in these open sandy areas remain at risk of submersion, which can suffocate the embryos (Whitmore & Dutton, 1985). Whitmore and Dutton (1985) suggested that this nesting behaviour is partly due to the physical constraints imposed by the large size of leatherback turtles, which preventing them from accessing more forested areas. Conversely, hawksbill turtles appear to prefer nesting in or near forested areas. Our micro habitats analysis revealed that female hawksbill turtles often select wooded forests with sparse creeping plants and bushes (M4, see Annexe I in supplementary data online at https://doi. org/10.1016/j.jnc.2025.127124). Such vegetation, characterized by a dense canopy, provides essential shading that mitigates the effect of solar radiation on nests temperature (Janzen, 1994; Hernandez-Cortes et al., 2018). In fact, we observed that 63 % of hawkbill nests were located in the forest, including 50 % in M4, a finding consistent with previous studies on Caribbean hawksbill (Horrocks & Scott, 1991; Kamel & Mrosovsky, 2005; Serafini et al., 2009). Likewise, Hernandez-Cortes et al., (2018) demonstrated that a vegetation cover of 29 %, composed exclusively of trees and similar to M4, resulted in significantly higher hatching (97.1 %) and emergence (96 %) rates, with an average nest temperature of 30.46°C (± 2.32°C) at Chenkan Beach, Mexico.

We demonstrated that hawksbill turtles exhibit individual-specific nesting areas, averaging 2 931 m², with a standard deviation of ± 2 695 m². Although there is a significant variability in these size sites, this variability modest compared to overall beach areas-such as Madiana (~8 350 m²), Diamant (~124 580 m²) and Salines (~62 535 m²). Our data further suggest that smaller—and presumably younger—hawksbill turtles tend to utilize more limited nesting areas. This may be attributed to the physiological stress experienced during their initial nesting seasons, potentially constraining their ability to explore broader areas in search of optimal nesting sites (Valverde et al., 1999). The generated polygons represent the spatial extent of each female's nesting activity, with an average nesting area of 2,931 ± 2,695 m². We investigated whether turtle size, measured as curved carapace length (CCL), influenced habitat use. However, no statistically significant correlation was detected.

In addition to spatial variability, we observed individual differences in the timing of arrival at the beach (the exact time the turtle lands on shore) for hawksbill turtles. On average, we observed that, a turtle returns to nest 1h13 ± 40 min after its previous recorded water emergence, underscoring both behavioural adaptation and temporal variability that warrant further investigation. For leatherback turtles, our results do not reveal clear individual-specific behaviours in nesting site selection or timing. This may be due to limited observational data concerning the areas used and the timing of arrival. Nevertheless, leather back turtles are known for their mobile nesting behaviour; previous studies have documented that this species can nest on different beaches, or even on separate islands within the same or across nesting seasons (Dutton et al., 2013; Molfetti et al., 2013; Horrocks et al., 2016). Regarding hawksbill turtles, natal philopatry with nest site fidelity are commonly observed (Bass et al., 1996), exceptions indicate some flexibility in nesting beach selection (Diamond, 1976; Esteban et al., 2015; Iverson et al., 2016). This behavioural plasticity could affect both the apparent remigration interval and regional population counts.

Anthropogenic pressures can also influence nesting behaviours on the studied beaches. A related study conducted on the beaches of Madiana, Diamant, and Salines demonstrated that artificial lighting, human activity, and habitat alterations have a detrimental impact on sea turtle nesting behaviour. The findings suggested that in areas with elevated levels of light and noise pollution, as well as frequent human presence, females, particularly leatherbacks, were more likely to abandon nesting attempts or refrain from emerging from the sea. These disturbances were also associated with a significant decline in nesting success and disruption of key nesting phases (Vanleynseele, 2024). Similar findings in other studies (Cayol, Maillard & Dubief, 2008; Calcagno, 2017; UICN, 2020) underscore the need for targeted conservation measures, such as reducing light pollution during nesting periods, and implementing revegetation plans based on turtle habitat preferences. In certain instances, local authorities have begun implementing measures in response. For example, in Schoelcher, the municipality now turns off the volleyball court lights—which illuminate the entire beach—around 10:00 p.m. each night, and they remain off unless players are present. While addressing light pollution is a positive step, broader climate resilience efforts remain crucial. The increasing frequency and severity of extreme weather events, such as hurricanes, pose significant threats to both sea turtle nests and beach stability. To safeguard the long-term viability of nesting habitats, site-specific strategies should be adopted, including nest relocation protocols, post-storm nest evaluations, and erosion control through the use of natural vegetation buffers. Such data-driven strategies are critical for the long-term survival of these vulnerable species.

Finally, our study supports the continued use of photoID as a valuable, non-invasive tool for monitoring sea turtle populations. Although software like I3S is highly effective, its performance can sometimes be limited by variations in photo quality angle, and distance (Dunbar et al., 2014; Calmanovici et al., 2018; Steinmetz et al., 2018). Nevertheless, photoID remains significantly less intrusive than traditional methods, such as handling and capture, which can cause stress, nest abandonment, or delayed nesting (Murphy, 1985; Jacobson & Lopez, 1994) and is cost effective compared to tagging methods (Buonantony, 2008).

2.7 CONCLUSION

To refine the characterization of Caribbean and Martinique sea turtle populations, expanding the existing photoID databases would be highly beneficial. These enhancements should include not only males inhabiting coastal waters but also turtles from neighbouring islands and leatherback turtles that migrate further north in the Atlantic after nesting. Furthermore, it is crucial that these databases be updated annually to maintain accurate records. In conservation efforts, population counts are often based on nighttime monitoring of nesting females (Santos et al., 2021). However, misidentifying remigrant turtles as first-time nesters can lead to significant overestimations of population levels. For instance, our observations indicate that 61 % of the leatherback turtles encountered on the three studied beaches in Martinique were individuals previously photographed during the same season. Additionally, the study also revealed that hawksbill turtles exhibit specific microhabitat preferences, providing valuable insights for habitat resto ration and revegetation plans. In Madiana, for example, while the wooded area hosts the highest concentration of nests, its limited size has led to instances where females dig up nests of others. This observation underscores the critical role that habitat quality plays in the preservation of these emblematic species. Ultimately, while our study offers site- specific insights, it contributes to a growing body of evidence supporting the need for coordinated, regional conservation policies that address both nesting beach protection and marine habitat use throughout the turtles' migratory range.

CHAPITRE 3

DES BIOFILMS DE CARAPACE AUX COQUILLES D'ŒUFS : EXPLORATION DE LA DIVERSITÉ ALGALE ET DES MÉTAUX TRACES CHEZ LES TORTUES MARINES *ERETMOCHELYS IMBRICATA* ET *DERMOCHELYS CORIACEA*

3.1 RESUMÉ

Les tortues marines, qui sont des espèces menacées, jouent un rôle fonctionnel majeur au sein de leur écosystème. Il est donc essentiel d'améliorer nos connaissances à leur sujet et de développer des méthodes de suivi et de recherche non-invasives, simples à mettre en œuvre et peu coûteuses dans un but de conservation de ces espèces. Nous explorons dans cette étude deux traceurs, (1) l'analyse métagénomique des organismes chloroplastiques du biofilm des carapaces de tortues, avec l'utilisation du marqueur chloroplastique 16S, et (2) l'analyse des concentrations en éléments traces métalliques (ETM) dans les coquilles d'œufs vides et le substrat du nid au moyen d'un spectromètre de masse par plasma à couplage inductif (ICPMS). Notre étude compare deux espèces de tortues marines : la tortue luth (*Dermochelys coriacea*) et la tortue imbriquée (*Eretmochelys imbricata*) en ponte sur l'île Caribéenne de la Martinique. Nos résultats révèlent un clivage interspécifique, tant dans la composition du biofilm que dans les profils d'ETM des coquilles d'œufs. On observe également une quasi-absence d'organismes chloroplastiques dans le biofilm des tortues luth. Les différences de composition de biofilm observées pourraient être attribuées à des différences comportementales, d'habitat et de la morphologie même des espèces. Aucune contamination des coquilles d'œufs par le substrat du nid n'a été détectée, suggérant que le transfert maternel est la source principale d'ETM. Les écarts entre espèces semblent liés à leur niveau trophique, la tortue imbriquée bioaccumulant généralement moins que la tortue luth. Enfin, cette étude exploratoire a permis la validation de méthodologies ouvrant la voie

pour vers de futures recherches comme l'étude de la variation individuels au sein d'une même espèce, ou le potentiel lien entre le biofilm et la santé des tortues marines.

Mots-clés : Biofilm, Eucaryotes chloroplastiques, Coquille d'œufs, Eléments traces, *Dermochelys coriacea*, *Eretmochelys imbricata*, Tortues marines.

Cet article, intitulé « From carapace biofilms to eggshells: exploring algal diversity and trace metals in the sea turtles *Eretmochelys imbricata* and *Dermochelys coriacea* », est prévu pour une soumission dans le journal *Marine Ecology Progress Series*. En tant que première auteure, j'ai contribué à l'essentiel de la recherche sur l'état de la question, au travail de terrain, à l'analyse des résultats et à la rédaction du manuscrit. Les Professeurs Réjean Tremblay, Benjamin de Montgolfier et El Mahdi Bendif ont fourni l'idée originale, ils ont aidé à la recherche sur l'état de la question, ainsi qu'au développement de la méthode et à la révision de l'article. Le professeur Richard St-Louis a également aidé au développement de la méthodologie et des analyses de métaux traces. Les professeurs Benjamin de Montgolfier et Réjean Tremblay ainsi que le chercheur Erwann Fraboulet ont permis l'acquisition des fonds. Les résultats de cet article ont été présentés à la réunion annuelle de Ressources Aquatiques Québec en 2025 ainsi qu'à la conférence Ecotoxicomic 2025 (Paris).

FROM CARAPACE BIOFILMS TO EGGSHELLS : EXPLORING ALGAL DIVERSITY AND TRACE METALS IN THE SEA TURTLES *ERETMOCHELYS IMBRICATA* AND *DERMOCHELYS CORIACEA*

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3.2 ABSTRACT

Sea turtles play a major functional role in their ecosystems, yet they are endangered species. It is therefore essential to improve our knowledge about them and to develop non-invasive, simple, and inexpensive monitoring and research methods to support their conservation. In this study, we explore two tracers: (1) metagenomic analysis of chloroplast organisms in the biofilm of turtle shells, using the 16S chloroplastic marker, and (2) analysis of trace metal elements (TMEs) concentrations in empty eggshells and nest substrate using inductively coupled plasma mass spectrometry (ICP-MS). Our study compares two species of sea turtles: the leatherback turtle (*Dermochelys coriacea*) and the hawksbill turtle (*Eretmochelys imbricata*) nesting on the Caribbean island of Martinique. Our results reveal an interspecific separation, both in biofilm composition and in trace elements (TMEs) profiles of eggshells. We also observed a near absence of chloroplast organisms in the leatherback turtle biofilm. The observed differences in biofilm composition could be attributed to differences in behaviour, habitat, and even the morphology of the species. No contamination of eggshells by nest substrate was detected, suggesting that maternal transfer is the primary source of TMEs. The differences between species appear to be related to their trophic level, with hawksbill turtles generally bioaccumulating less than leatherback turtles. Finally, this exploratory study has validated methodologies that pave the way for future research, such as the study of individual variation within the same species, or the potential link between biofilm and the health of sea turtles.

Keywords : Biofilm, Chloroplastic eukaryotes, Eggshell, Trace elements, *Dermochelys coriacea*, *Eretmochelys imbricata*, Sea turtle.

3.3 INTRODUCTION

Sea turtles are considered as keystone species and ecosystem engineers by grazing on seagrass beds, regulating jellyfish or sponges, and transporting nutrients between the ocean and beaches (Liu, 2017; Hendrix & Pérez-Espona, 2024). This ecological importance justifies their long-term monitoring and targeted conservation actions (NOAA, 2021). Sea turtles are bound to migrate from foraging grounds to nesting beaches to reproduce, typically every 2 to 7 years (Price et al., 2004; Chevalier, 2005). Our study aims to explore two complementary indicators of potential differentiation of migration: the sea turtles carapace biofilm composition; and the trace metal composition of their eggshells through two different sea turtle species, the leatherback (*Dermochelys coriacea*) and the hawksbill (*Eretmochelys imbricata*).

A biofilm is a complex microbial community adhering to a living or inert surface, organised into microcolonies and encased within a self-generated extracellular polymeric substance (EPS) Myckatyn et al., 2016; Ventura et al., 2024). This organization confers upon the cells a sessile, structured lifestyle that is highly tolerant to stress (antibiotics, host defences, hydrodynamics) (Costerton et al., 1999; Hall-Stoodley et al., 2004). The EPS matrix, composed primarily of polysaccharides, proteins, nucleic acids, and lipids, play key roles such as nutrient trapping, enzyme retention, protection, and mechanical cohesion. This explains the persistence and resilience of biofilms in various environments (Flemming & Wingender, 2010). In the marine environment, any submerged surface is rapidly colonized; the carapace of sea turtles thus acts as a biotic substrate where bacteria and microalgae settle, forming a dynamic biofilm, a true gateway to more complex epibioses (Dang & Lovell, 2016). It accumulates over time, and the species that compose it are partly determined by the host species (Rivera et al., 2018; Keller et al., 2021; Riaux-Gobin et al., 2021) and environmental conditions crossed by the host (Majewska et al., 2017; Van de Vijver et al., 2020; Loghmannia et al., 2021; Riaux-Gobin et al., 2021; Kanjer et al., 2022). Indeed, the composition of the biofilm can vary with temperature, salinity, productivity, and the chemistry of the water masses, as well as with local ecological interactions (Raghupathi et al., 2018; Mai et al., 2020; Fathollahi & Coupe, 2021; Pinel et al., 2021). Although exceptions exist, such as Chelonicola and Poulinea, many of the diatoms observed are likely benthic species collected incidentally in the turtles' foraging areas (Rivera et al., 2018). Studies on epiphytic diatoms show that the epibiotic diatom communities may vary greatly depending on geographical locality and external environmental conditions (Majewska et al., 2015a; Robinson et al., 2016; Majewska et al., 2017). Thus, analysing the biofilm present on the carapace of sea turtles can reveal environmental signatures and, indirectly, provide information about the habitats traversed and the pressures encountered.

Trace metal elements (TMEs) are inorganic elements naturally present in the environment, but their scientific and societal importance is increasing as the impact of human activities intensifies contamination and their concentration in the natural environment (Ross et al., 2017; Chan, 2024). Biologically, a distinction is made between essential elements such as Fe, Zn, or Se, which are indispensable but toxic above certain thresholds; and non-essential elements such as Hg, Pb, or Cd, which are toxic even at low concentrations (Shaw et al., 2020; Arienzo, 2023). Sea turtles are no exception; they are frequently exposed to and bioaccumulate TMEs through multiple ways, particularly by feeding (Ross et al., 2017; Chan, 2024). Another source of contamination is the immediate environment through direct absorption from the water in the turtles' feeding areas, which strongly influences the observed levels of trace metals, with increased exposure near industrialized or contaminated coastal areas (Komoroske et al., 2011; Chan, 2024; Hrizi et al., 2024). Females can transfer some of the accumulated elements to their offspring: maternal transfer to the eggs (Guirlet et al., 2008; Ehsanpour et al., 2014; Ross et al., 2016). The dynamics of trace elements in sea turtles often describe a chain-like trajectory: from the environment to the female, from maternal tissues to the egg during vitellogenesis and pre-laying calcification, and then, after laying, possible secondary exchanges with the sand and interstitial water (Sakai et al., 1995; Guirlet et al., 2008; Ehsanpour et al., 2014; Ross et al., 2017; Jian et al., 2021; Tanabe et al., 2022). Numerous studies highlight correlations between maternal burden and the different fractions of the egg, confirming the transfer of essential elements (Zn, Cu, Se, Fe) and, in some cases, toxic elements (Hg, Pb, Cd) (Guirlet et al., 2008; Van de Merwe et al., 2010; Ehsanpour et al., 2014; Dennis et al., 2020; Jian et al., 2021; Tanabe et al., 2022; Ahmadi et al., 2024; Jian et al., 2024). Post-laying exchanges remain plausible thanks to the permeability of the membranes may allow for the absorption of metals from the incubation environment (Hewavisenthi & Parmenter, 2001; Dennis et al., 2020; Jian et al., 2021; Tanabe et al., 2022). However, many studies do not observe measurable enrichment and attribute most of the observed contamination to maternal transfers (Guirlet et al., 2008; Ehsanpour et al., 2014; du Preez et al., 2018; Dennis et al., 2020; Guzman et al., 2020). From this perspective, multi-elemental profiles obtained by ICP-MS on eggshells collected after hatching constitute a minimally invasive marker to reflect the past exposure of females to the environments they frequented, their life history, compare populations, and inform management and conservation priorities for nesting beaches.

Our two exploratory approaches allow us to combine the "microbial map" of the biofilm and the "elemental signature" of the eggshells, opening a new window onto the spatial and trophic ecology of *Eretmochelys imbricata* (hawksbill turtle) and *Dermochelys coriacea* (leatherback turtle). Our preliminary study aims to test the feasibility of this multi-tracer framework, to identify the most informative indicator elements and taxa, to define non- or minimally invasive sampling protocols, and to generate hypotheses regarding the production of knowledge useful for the management and conservation of these species. We hypothesised that both microbial and metallic profiles would differ across species, individuals, and potentially among sites. Convergent or divergent patterns between these two markers are expected to provide insights into habitat overlap and differentiation. The aim of this study is therefore twofold: first, to lay the groundwork for a multi-marker framework, and second, to assess whether microbial biofilm composition and eggshell metal profiles, considered separately or in combination, can capture individual variability in movement patterns. We propose these markers as novel complementary tools. Specifically, we hypothesise that the taxonomic composition of biofilms reflects the ecological settings experienced by hosts, as supported by recent advances in metagenomics and microbial ecology, while the incorporation of metals into eggshells records trophic exposure of females across visited habitats.

3.4 MATERIALS AND METHODS

3.4.1 Study Site

The hawksbill and leatherback sea turtles were sampled in Martinique, in the South of the Caribbean Sea (Fig. 23). This study focuses on three major nesting beaches, chosen for their gradient of anthropogenic perturbation and described in Langel et al. (2025a). The three beaches are Madiana, located near the capital and considered as the most anthropogenic impacted beach, Diamant near a small town and intermediate level of human frequentation and Salines, more isolated and without light pollution and human activities during the night.

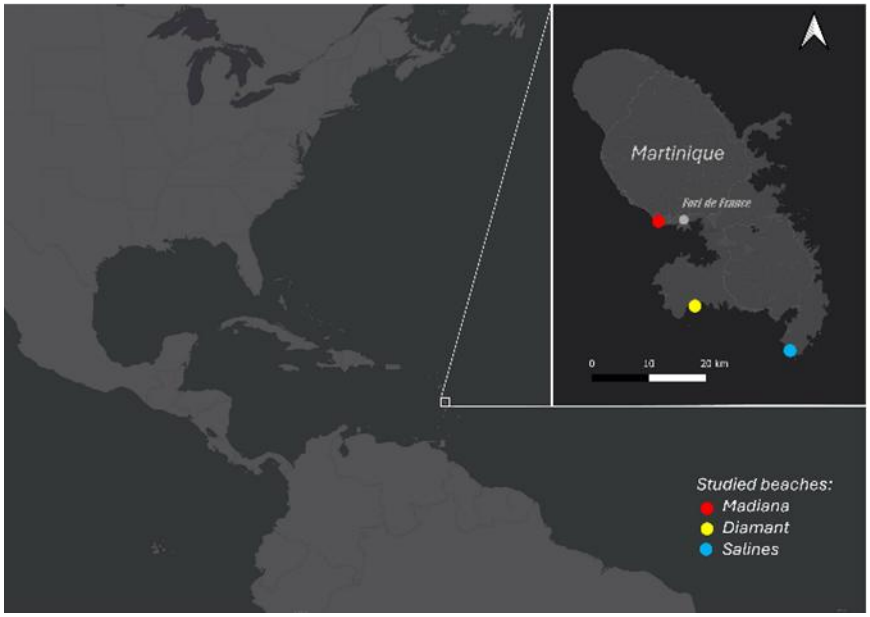

Figure 23. Martinique and the studied beaches.

3.4.2 Biofilm Sampling

Biofilm were collected by night patrols of the nesting sea turtle, between May and June 2024 on 11 different turtles, six hawksbills (one from Salines and five from Diamant) and five leatherbacks (four from Salines et one from Diamant). Sampling was carried out under red lights, during egg-laying by scraping standardized areas of the carapace (**Fig. 24**), using sterile toothbrushes, hairnet, mask and gloves. Each biofilm sample was placed directly in 40 ml ethanol (Falcon tube) refrigerated until -20° preservation at arrival in the laboratory.

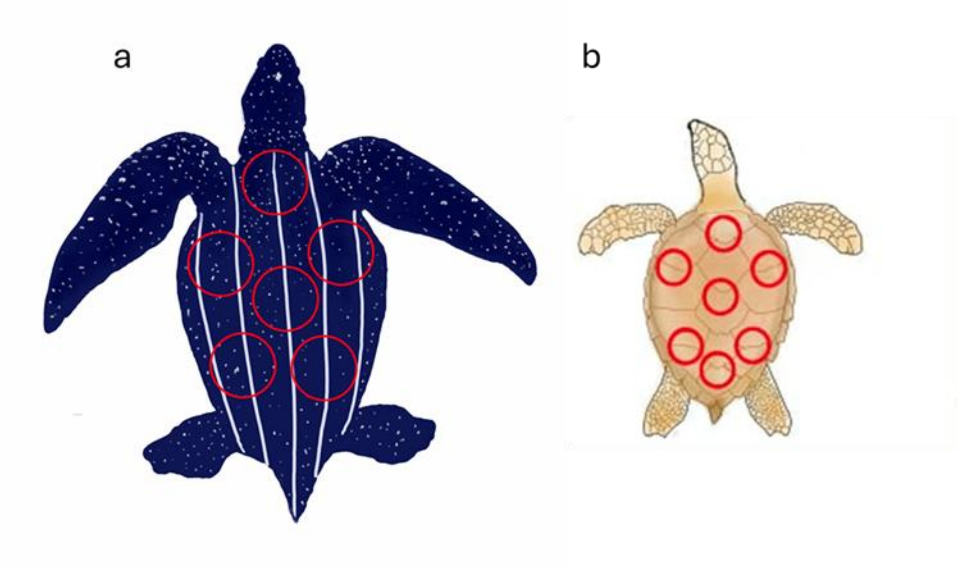

Figure 24. Biofilm sampling areas on (a) leatherbacks and (b) hawksbills turtles.

DNA extraction and bioinformatic pipeline were applied by Génome Québec sequencing platform using the DNeasy PowerBiofilm by Qiagen. DNA samples were PCR-amplified targeting the universal 16S rRNA V4–V5b region using primer pair 515FB (5′-GTGYCAGCMGCCGCGGTAA-3′) and 926R (5′-CCGYCAATTYMTTTRAGTTT-3′) (Parada et al., 2015; Walters et al., 2015). This primer set provides broad coverage across Bacteria (85-95%), Eukarya (81–94%), mitochondrial lineages (57–77%), and chloroplastic sequences (81–93%), the latter aligning with the objectives of this study. Forward and reverse paired-end sequences were assembled for each of the 11 samples. Specifically, paired reads retained for downstream analysis were aligned to form a contig. Within contigs, individual sequences with any mismatch or any sequence having at least one position with a quality value < 30 were discarded. Retained sequences were grouped, assigned and clustered into operational taxonomic units (OTUs) based on the Pr2 (v4.14.0; Guillou et al., 2013) reference database. Prior to sequence assignment, chimera checks were undertaken using usearch61 (via vsearch 1.11.1). After detection and removal of chimeras, the remaining amplicons were compared to the PR2 (v4.14.0) reference database. After filtering, sequences with ≥ 97% identity were considered conspecific and clustered into OTUs using QIIME 1.9.1 pick_otus (pickOTU; usearch61_ref via vsearch 1.11.1). For each OTU, the most abundant sequence was retained as the representative sequence. These representative sequences were then compared to the PR2 (v4.14.0) database for taxonomic assignment using the naive Bayesian classifier of mothur 1.48, called through QIIME 1.9.1 with assign_taxonomy (assigned.py-mothur). For this study, we focused on OTUs from chloroplastic eukaryotes.

The study of the biofilm associated microalgae epiotic was conducted using sequencing data processed and analysed using R Statistical Software (V.4.5.1; R Core Team 2025). Results were assessed by rarefaction and abundance distribution curves, enabling validation of the representativeness of the observed communities. Classical richness and diversity indices were then calculated using a Wilcoxon test, while the taxonomic structure was illustrated by stacked bar graphs representing the dominant taxa. Variability between individuals and between species was explored using multivariate analyses and specific visualizations (heatmap, Krona representation of Class and Order of the chloroplastic eukaryotes). Finally, a principal component analysis (PCA) was applied to visualize differences between the two sea turtle's species.

3.4.3 Elemental Signature

Eggshells samples were collected, after Beryl's hurricane in July 2024 (Langel et al., 2024). Hawksbill eggshells, from 26 individuals were collected, from Salines (11), Madiana (3) and Diamant (12). Leatherback eggshells were obtained only on Salines from 17 individuals. Eggs were differentiated through size and the location of the nest. Eggs were then cleaned from any organic matter with distilled water, left for approximately 10 to 20 minutes at 100°C till completely dry and grinded with a mortar and pestle. Sand samples were collected near 9 sea turtles' nests in Salines, 15 in Diamant and 8 in Madiana. Samples were rinsed with distilled water and dried at 100°C for 20 minutes. Eggshells sample (100mg) were digested with 1.6ml of nitric acid (HNO_3, 65%) and 0.8ml hydrogen peroxide (H_2O_2, 30%) for 12h at 30°C on a dry bath incubator. Sand samples (500 mg) has been digested with 2 ml of hydrochloric acid (HCl, %) and 6 ml of nitric acid (HNO_3, 65%) and heated in an Anton Paar Multiwave 5000 at 168°C for 18min; then raised up to 175°C in 3 minutes and kept at 175°C for 4 minutes. Four technical replicates were randomly selected and processed under the same treatment as all samples to evaluate the analytical precision using relative deviations (RPD%) and the Relative Standard Deviation Percentage (RSD%) (see Annexe I). Eggshell samples were diluted 1:50 and sand samples 1:500 in Milli-Q water acidified to ~2% with nitric acid (v/v). Given the high Calcium (Ca) and Magnesium (Mg) concentrations, aliquots for elemental analysis were further diluted 1:25,000 and 1:5,000, respectively.

Digested eggshells and sand samples were analysed by inductively coupled plasma interfaced to a triple-quadrupole mass spectrometer ICP-QQQ-MS, Agilent 8900, equipped with a MicroMist nebulizer. Plasma power was set at 1540W, RF matching at 1.75V, gas carrier and makeup gas 1.06 and 0.10 L/min respectively, nebulizer pump was set at 0.12 rps. Samples were introduced in the plasma interface via an ASX 520 autosampler from CETAC. Element signals were acquired for 200 msec per mass and three acquisitions were realized. The element quantification was performed in normal mode with a seven-point external calibration using Multi-Element V for ICP (Fluka Chemie Gmbh, Switzerland) with a concentration range between 0.10 and 50.00 ng.ml-1 for Manganese (Mn), Aluminium (Al), Chromium (Cr), Cadmium (Cd), Molybdenum (Mo), Vanadium (V) and Iron (Fe) was ranging from 1.0 to 500 ng.ml-1. Arsenic (As) was quantified with a seven-point external calibration plot using a single element calibration solution (JT Baker, Philisburg, New Jersey, USA) with a concentration range between 0.05 and 20.00 ng.ml-1. Rare earth metals were quantified from multielement 1 solution from SPEXCertiPrep with concentration ranging from 0.50 to 200.00 ng.ml-1. Performance of the extraction method was assessed by the analysis of a certified reference material standard (FEBS-1 (Clancy et al, 2005) and 1944 (NIST, 2017)), and a procedural blank. Performance of the instrument was monitored by quality control (QC) solution of known metal concentration, every 20 samples, throughout sequences. Control of the system, acquisition and data processing were carried out with the Agilent ChemStation software. Limit of quantification in final solutions for Fe and Al were 2.0 and 1.0 ng.ml-1 respectively and 0.5 ng.ml-1 for Mn, Cr, Cd, Mo, V, Lanthanum (La), Cerium (Ce), Praseodymium (Pr), Samarium (Sm), Europium (Eu), Gadolinium (Gd), Terbium (Tb), Dysprosium (Dy), Holmium (Ho), Erbium (Er), Thorium (Th), Yttrium (Y), Lutetium (Lu), Neodymium (Nd), Scandium (Sc), Thulium (Tm), Ytterbium (Yb) and 0.1 ng.ml1 for As.

All statistical analyses were conducted exclusively in R (v4.5.1; R Core Team, 2025). After Euclidean distances transformation, PCA was applied. To evaluate the potential elemental composition difference between eggshells and sand measurements, a PERMANOVA has been done on Salines samples, being the only beach with both hawksbills and leatherbacks eggshells. Finally, we also checked the homogeneity of multivariate dispersions between groups using the betadisper function, applied to the Euclidean distance matrix used for PERMANOVA.

3.5 RESULTS

3.5.1 Biofilm Composition in Eukaryotes

3.5.1.1 Alpha-diversity baselines: rarefaction, abundance distributions, and core indices.

A total of 241 eukaryotic OTUs were identified. The overall rarefaction curve quickly reaches a plateau, indicating that most of the OTU richness has been captured at the observed sequencing depths (**Fig.25**). However, regarding the leatherback turtle, OTU richness is very low and does not reach a plateau, therefore, it is the diversity of hawksbill turtles that drives the overall diversity pattern. The rank-abundance curve shows a rapid decrease in relative abundance, indicating low evenness and limited richness (see **Fig.30a** in Annexe II). This trend is confirmed by the abundance class histogram (see **Fig. 30b** in Annexe II), where most reads are concentrated in the biggest abundance class.

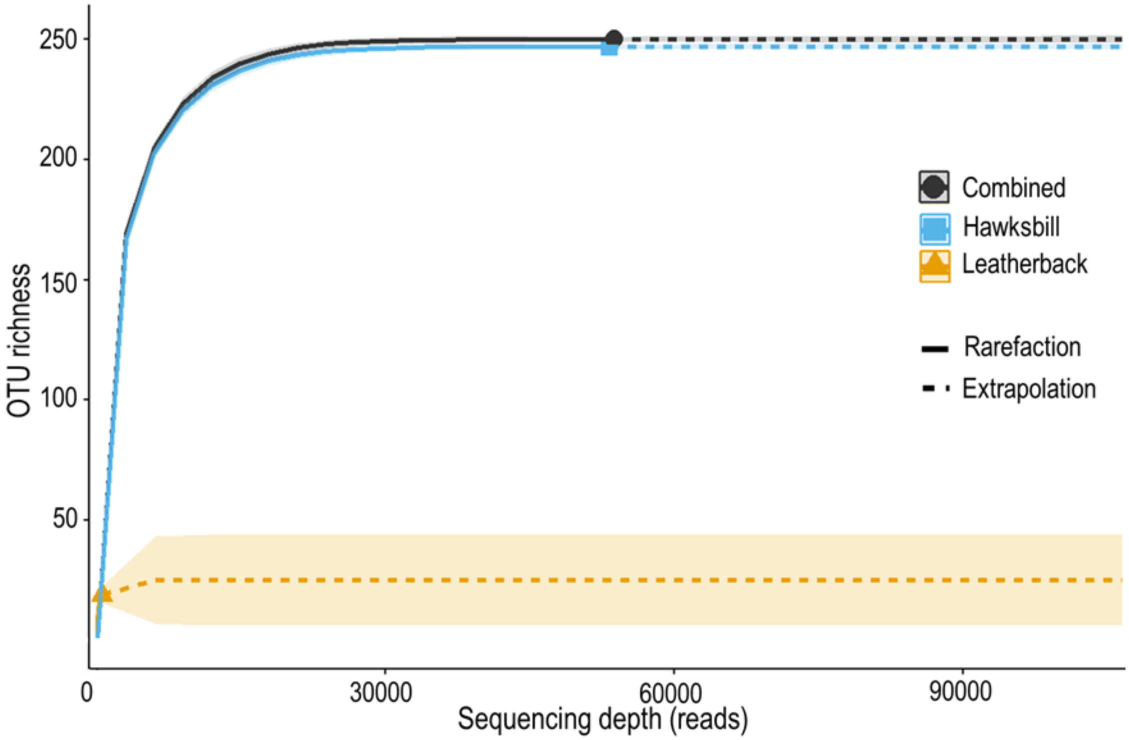

Figure 25. OTUs richness accumulation curve as a function of sequencing depth in reads.

Alpha-diversity differed markedly between species (**Fig. 26**). Biofilm on hawksbills carapace showed higher species richness values estimated by Chao1 (Wilcoxon test = 0), larger size effect (Cliff's δ = 1, 95% CI [0.86; 1]), higher evenness (Wilcoxon test = 18; R^2 = 0,61), richness (Wilcoxon test = 30) and Shannon diversity (Wilcoxon test = 30; R^2 = 0.87) than the biofilm collected on the carapace of leatherbacks turtles. The species explained 82.5% of the variance in richness (R^2 = 0.83). However, the Simpson diversity index of biofilm (1–D) did not differ significantly between species (Wilcoxon test = 18).

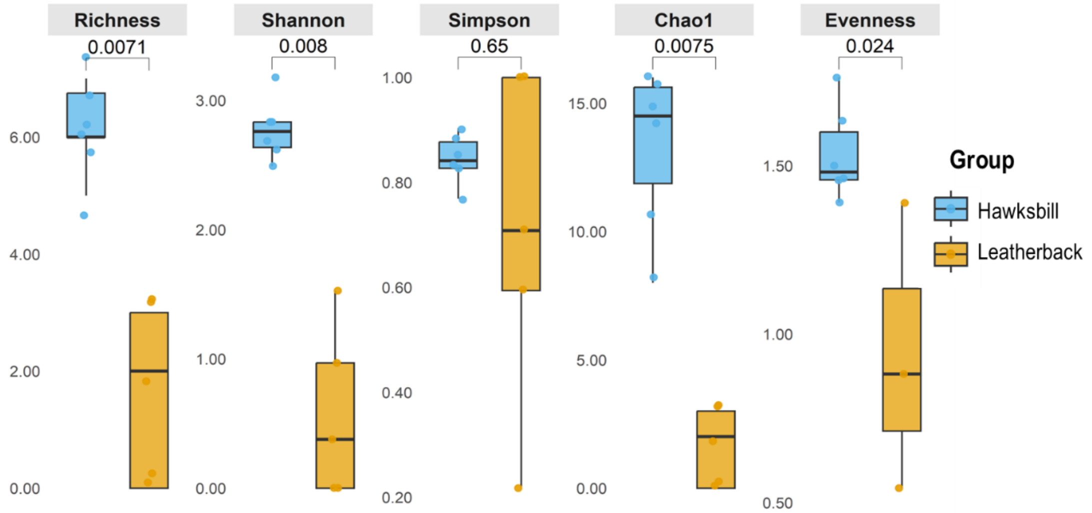

Figure 26. Boxplots of alpha-diversity metrics (Chao1, Evenness, Richness, Shannon, Simpson) comparing hawksbills vs. leatherbacks and their p-values.

3.5.1.2 Diversity and dominant taxa

We identified that the most prevalent group of photosynthetic eukaryotes was diatoms. Out of our 241 OTUs, 189 (79.4%) were assigned to diatoms (*Bacillariophyta*; **Fig. 27a**). Within this group, *raphids* represent 64 assignments (25.6% of the total and 33.7% of the diatoms), *centrics/mediophytes* 15 assignments (6.0% of the total and 7.9% of the diatoms), and 111 assignments are unspecified diatoms (44.4% of the total and 58.4% of the diatoms). The second dominant group was the brown algae *Phaeophyceae* with 8 OTUs (~3.3% of all OTUs), followed by the red algae *Florideophyceae* (13 OTUs, ~5.4%) and the green algae *Ulvophyceae* (5 OTUs, ~2.1%). The less important groups were mainly composed of *Pinguiophyceae*, *Pelagophyceae*, and *Pavlovophyceae* (each ≤5 OTUs), with smaller contributions from *Embryophyceae*, *Chlorodendrophyceae*, *Prymnesiophyceae*, *Chlorarachniophyceae*, *Cryptophyceae*, *Compsopogonophyceae*, and *Colpodellidea*. However, any eukaryotes were found in two leatherbacks samples (samples n°3 and n°4, **Fig. 27c**). Through Sunburst diagram analyses, the biofilm composition was almost similar to the hawksbill's samples (with ~79% *Bacillariophyta* with *Phaeophyceae*, *Florideophyceae* and

Ulvophyceae) (**Fig. 27a**), while all leatherback turtle samples had 0.1% of the total composition in eukaryotes across all samples (see **Fig. 31** in Annexe III).

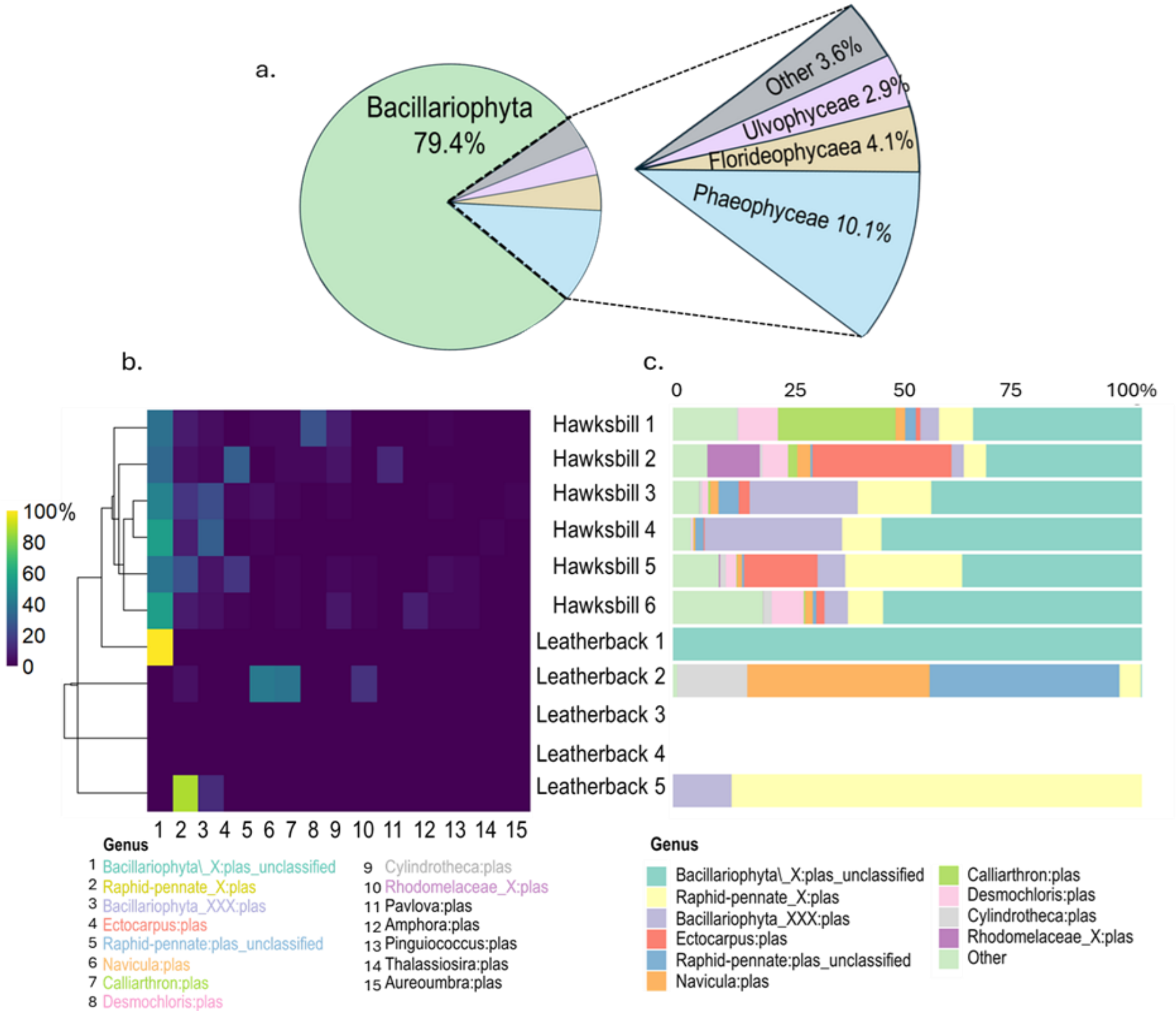

Figure 27. Taxonomic composition of chloroplastic eukaryotes communities. **(a)** Taxonomic diversity across a Sunburst diagram. The rings represent different levels in the phylogenetic tree of eukaryote Class. Leatherback contributing up to ~0.1% of this sunburst in Bacillariophyta. **(b)** Heatmap of relative abundances and clustering of eukaryotic genera in hawksbills and leatherback samples. Colour intensity indicates relative proportion per taxon and per sample in relative abundance (%). **(c)** Taxonomic composition profiles per sample at the genus level for eukaryotic communities from biofilm samples of hawksbills and leatherbacks. Each bar shows the relative proportion of each genus within the sample.

3.5.1.3 Individual and inter-species variability

In the relative abundance representation (**Fig. 27b**), several OTUs appear dominant, suggesting variations in samples compositions. Absolute values (see **Fig. 32** in Annexe IV) showed an increase in the total microbial load in certain samples, with few taxonomic rearrangements, indicating that the observed differences mainly reflect the overall quantity rather than a true overabundance of specific OTUs. The inter-specific difference was striking (**Fig. 27b, 27c** and **Fig. 28**) with large presence of the *Bacillariophyta_X:plas_unclassified* (**Fig. 27b** and **27c**). The hawksbills samples showed a richer and more balanced community, where several diatom groups (*e.g.*, *Rapid-pennate_X:plas*, *Bacillariophyta_XXX:plas*) coexisted at medium levels, while some brown or green algae (*e.g.*, *Ectocarpus*, *Tetraselmis*) were detected only at trace levels. Conversely, the leatherback biofilm was more contrasted without eukaryotes in some samples and large abundance of *Navicula:plas* or *Rapid-pennate_X:pla* and *Bacillariophyta_XXX:plas* in other samples. Thus, hawksbills appear to host more stable and diverse assemblages dominated by diatoms, while leatherbacks alternate between weak signals and punctate blooms of a single taxon. The majority of other listed taxa (*e.g. Fucus*, *Pinguioococcus*, *Pavlova*) remained rare and without overall influence structure. This observation was confirmed by the PCA revealing important differences in the composition of eukaryotic communities between the biofilm composition from hawksbills and leatherbacks (**Fig. 28**).

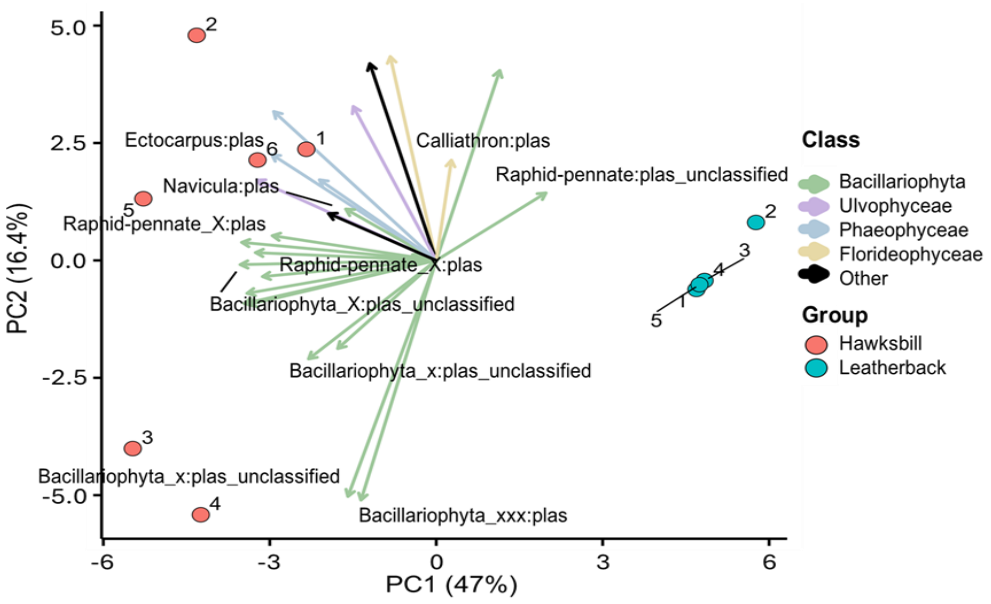

Figure 28. PCA of the hawksbill (n=6) and leatherback (n=5) samples and the taxa Classes.

3.5.2 Eggshell Trace-Metals Elements Profiles and Species-Level Variation

3.5.2.1 Trace metals elements profiles

Concentrations of 45 elements were determined in eggshell samples (**Table 5**). According to a common convention in geochemistry, major elements show values >1% (10,000 µg/g), minor elements between 0.1–1% (1,000–10,000 µg/g) and trace elements <0.1% (<1,000 µg/g) (Jenner, 1996), hawksbill eggshells were dominated by Ca, reflecting its calcite matrix, with phosphorus (P) and Mg as minor elements. Among the trace elements, strontium (Sr) was notable following by Fe, copper (Cu), and zinc (Zn). The presence of barium (Ba) and Cr remained low, and several potentially toxic elements such as lead (Pb), As and uranium (U), were present, but only in ultra-trace amounts. Hg, Pt and thallium were below the detection limit. Concerning leatherbacks samples, the elemental composition of eggshells was dominated by similar elements (Ca with minor contribution of Mg and P). The more important levels of trace elements were Na, Fe, Sr, Zn, Cu or Mn. Several elements appear only in ultra-trace amounts, for example lithium (Li), cobalt (Co), Se, Pb or U.

Table 5. Mean (ppm) and standard deviation (SD; ppm) of TMEs in eggshells of hawksbill (*E. imbricata*) and leatherback (*D. coriacea*) across the three study sites.

Eretmochelys imbricata							*Dermochelys coriacea*	
Beach	Madiana		Diamant		Salines			
Elements	Mean	SD	Mean	SD	Mean	SD	Mean	SD
7Li	0.04	0.05	0.26	0.20	0.06	0.05	0.09	0.12
9Be	0.01	0.01	0.01	0.02	0.01	0.02	0.01	0.01
11B	0.05	0.09	2.20	1.97	4.25	2.72	2.04	1.59
23Na	27.73	4.15	180.01	160.79	303.33	144.98	214.24	187.56
24Mg	197.71	182.81	1070.76	633.64	2043.05	1020.67	1297.25	888.01
27Al	14.33	6.55	31.00	16.52	33.25	24.23	22.75	24.46
31P	119.58	68.94	3873.62	7351.84	307.67	347.50	1120.15	1093.63
44Ca	26587.24	6647.97	89070.98	81579.48	104770.07	73534.53	60722.80	56105.03
47Ti	3.46	1.03	5.42	5.48	2.94	3.07	5.38	7.04
51V	0.05	0.08	0.21	0.36	0.27	0.29	2.10	3.61
52Cr	0.54	0.41	1.77	1.27	1.13	0.61	1.49	1.79
55Mn	20.17	21.24	8.64	7.89	5.34	3.44	47.39	169.02
56Fe	49.00	29.66	62.27	37.21	49.84	29.03	207.53	247.27
59Co	1.77	1.12	0.17	0.13	0.08	0.06	0.46	0.69
60Ni	0.54	0.64	0.84	0.85	0.64	0.40	3.25	5.63
63Cu	20.33	3.38	8.02	3.50	9.20	5.21	46.20	112.13
66Zn	9.44	15.81	15.26	31.65	3.99	4.04	55.64	74.48
72Ge	0.09	0.01	0.07	0.02	0.08	0.01	1.75	5.08
75As	0.00	0.00	0.37	0.57	0.12	0.13	1.61	2.41
78Se	0.67	0.78	0.69	0.91	0.29	0.55	0.51	0.77
88Sr	39.42	16.27	273.43	273.30	397.34	260.06	194.38	200.15
89Y	0.18	0.13	0.20	0.12	0.47	0.30	0.22	0.30
90Zr	0.21	0.23	0.14	0.22	0.08	0.15	0.15	0.46
93Nb	0.04	0.04	0.01	0.02	0.01	0.02	1.07	3.42
95Mo	0.00	0.00	0.22	0.59	0.09	0.11	1.82	2.76
101Ru	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
103Rh	0.00	0.00	0.01	0.01	0.01	0.01	0.57	2.46
105Pd	0.02	0.02	0.01	0.00	0.03	0.08	0.16	0.26
111Cd	0.00	0.00	0.02	0.06	0.00	0.00	0.06	0.11
118Sn	0.00	0.00	0.00	0.00	0.07	0.17	0.03	0.07
121Sb	0.01	0.00	0.02	0.02	0.01	0.01	0.02	0.01
125Te	0.00	0.00	0.01	0.02	0.00	0.00	0.00	0.00
133Cs	0.00	0.00	0.00	0.00	0.00	0.00	0.18	0.53
137Ba	0.66	0.82	1.70	1.64	0.80	0.38	1.32	1.26
178Hf	0.05	0.06	0.04	0.07	0.02	0.04	0.04	0.12
181Ta	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.02
185Re	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.02
193Ir	0.09	0.03	0.24	0.24	0.19	0.17	0.04	0.03
195Pt	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
197Au	0.03	0.04	0.01	0.05	0.01	0.02	0.00	0.00
202Hg	0.00	0.00	0.01	0.03	0.00	0.00	0.00	0.00
205Tl	0.00	0.00	0.00	0.00	0.00	0.01	0.14	0.43
208Pb	0.41	0.22	0.39	0.50	0.15	0.06	0.47	0.54
232Th	0.01	0.02	0.01	0.02	0.01	0.01	0.17	0.52
238U	0.17	0.05	0.18	0.12	0.41	0.19	0.50	0.46

3.5.3 Trace Metals Elements Analysis

The PCA of the trace elements in the eggshells showed a structure primarily driven by PC1 (21.8%), with a secondary contribution from PC2 (15.3%; **Fig.29**). PC1, was dominated by transition metals (*e.g.*, Fe, As, Mo, Ni, Ge) and the opposite side was associated mainly with alkaline earth metals and lithophile elements (LILEs; *e.g.* Ca, Sr, Ba, Rb). PC2 contrasted elements such as Mg, Ti, Al, Sb, Cu and Co, as indicated by the orientation of the vectors. At the interspecific level, Hawksbill clusters was predominant on the negative side of PC1 with a narrow, vertically elongated ellipse, while leatherbacks were more dispersed along PC1 around neutral to positive values. The 95% ellipses overlap, indicating real but moderate separation between species, mainly along PC1.

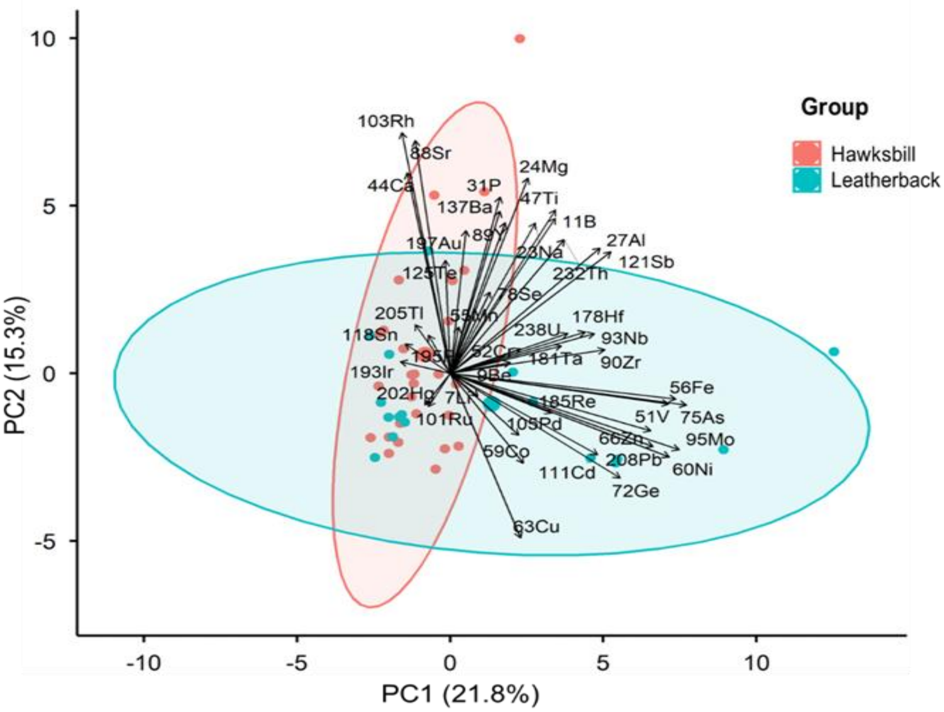

Figure 29. PCA of leatherbacks (blue) and hawksbills (red) eggshells (ell. 95%). Data transformed through an Euclidean matrix.

3.5.4 Beaches Trace-Element Profiles

3.5.4.1 Trace metals elements profiles

We calculated the concentrations of 45 elements in sand samples throughout the three study sites (**Table 6**). The average inter-beach profile of shells was dominated by Ca (major), accompanied by Mg, Al, Fe, Sr (minors) and a wide range of trace elements (Na, P, titanium (Ti), V, Cr, Mn, Co, Ni, Cu, Zn, barium (Ba), Pb, U etc.) and ultra-traces (boron (B), germanium (Ge), As, palladium (Pd), Hg etc.). The spatial contrasts were marked: Salines shows the highest concentrations of Ca, Mg, Sr, Na, P, and yttrium (Y), U, and several platinum-group elements (PGEs) in ultra-trace amounts (Rhodium (Rh), Pd, Iridium (Ir), Pt). Conversely, Madiana was significantly enriched in transition metals and lithophiles : Fe, Al, Ti, V, Mn, Co, Ni, Cu, Zn, as well as Ba, Pb, Th, and various trace elements (germanium (Ge), zirconium (Zr), niobium (Nb), Mo, Antimony (Sb), Tellurium (Te)), indicating a more terrigenous/detrital signature. Diamant exhibited maximal concentrations for only a small number of trace-elements such as Beryllium (Be), and High Field Strength Elements (HFSEs) like Hafnium (Hf) and Tantalum (Ta), as well as Tl, with generally intermediate or lower levels for the other elements comparatively to the two other beaches.

Table 6. Mean (ppm) and standard deviation (SD; ppm) of trace metal elements (TMEs) in the sand across the three study sites.

Beach						
Beach	Madiana		Diamant		Salines	
Elements	Mean	SD	Mean	SD	Mean	SD
7Li	4.88	2.92	2.50	0.63	3.47	0.89
9Be	2.86	0.18	2.90	0.14	2.88	0.15
11B	0.00	0.00	0.02	0.07	1.20	0.32
23Na	121.92	81.38	320.34	152.29	485.26	150.52
24Mg	1171.58	363.66	6289.36	2941.43	22076.24	2769.49
27Al	3969.71	2641.09	1633.02	728.36	1399.29	227.45
31P	308.04	67.25	348.39	72.72	492.06	70.38
44Ca	378.61	175.30	13803.55	5629.70	33653.44	4048.55
47Ti	1607.04	556.83	308.50	174.69	57.69	22.32
51V	113.61	43.99	23.09	18.75	1.37	1.14
52Cr	23.23	1.83	23.24	1.91	25.38	1.18
55Mn	275.63	117.79	69.40	31.57	81.69	15.58

56Fe	20411.79	5894.36	3481.16	1959.98	885.82	185.89
59Co	10.41	3.16	3.57	0.70	2.66	0.20
60Ni	2.56	1.55	1.84	3.70	0.58	0.72
63Cu	10.65	2.63	4.48	1.52	3.93	0.62
66Zn	64.75	23.61	5.22	5.30	0.29	0.53
72Ge	1.41	0.21	0.47	0.13	0.45	0.05
75As	0.00	0.00	0.00	0.00	0.82	0.54
78Se	0.00	0.00	0.00	0.00	0.00	0.00
88Sr	12.05	9.54	1526.37	603.43	2685.66	322.98
89Y	11.55	0.78	12.04	0.83	15.16	0.80
90Zr	1.22	1.23	0.65	0.40	0.15	0.21
93Nb	0.32	0.17	0.20	0.12	0.31	0.19
95Mo	0.29	0.14	0.08	0.14	0.14	0.11
101Ru	0.00	0.00	0.00	0.00	0.00	0.00
103Rh	0.01	0.01	0.04	0.02	0.07	0.01
105Pd	0.02	0.02	0.02	0.02	0.03	0.03
111Cd	0.00	0.00	0.00	0.00	0.00	0.00
118Sn	0.93	1.35	0.00	0.00	0.00	0.00
121Sb	0.09	0.06	0.03	0.02	0.05	0.01
125Te	0.02	0.02	0.02	0.02	0.02	0.03
133Cs	0.00	0.00	0.00	0.00	0.00	0.00
137Ba	15.54	14.20	5.78	2.58	6.79	1.21
178Hf	0.12	0.07	0.20	0.06	0.15	0.06
181Ta	0.04	0.01	0.05	0.02	0.05	0.01
185Re	0.00	0.00	0.00	0.00	0.00	0.00
193Ir	0.05	0.03	0.05	0.03	0.06	0.04
195Pt	0.00	0.00	0.00	0.00	0.01	0.01
197Au	0.28	0.27	0.18	0.25	0.30	0.34
202Hg	0.00	0.00	0.00	0.00	0.02	0.06
205Tl	1.82	0.09	1.83	0.06	1.81	0.09
208Pb	6.34	1.08	1.99	0.82	1.70	1.68
232Th	11.14	0.55	10.82	0.35	10.80	0.45
238U	10.01	0.54	10.77	0.43	11.45	0.47

A PERMANOVA based on a Euclidean distance calculated from the concentrations of common elements showed a significant effect of matrix type (sand vs. eggs) for both turtle species on overall chemical composition (adonis2, $R^2 = 0.459$, $F_{1,37} = 31.34$, $p = 0.0001$). The test for homogeneity of multivariate dispersions (betadisper) did not reveal a significant difference in dispersion between the groups ($F_{1,37} = 0.083$, $p = 0.775$), suggesting that the effect detected by the PERMANOVA primarily reflects a difference in the element's composition.

3.6 DISCUSSION

We hypothesised that biofilm microbial and elemental eggshell profiles could differ sufficiently across species, individuals, and nesting sites to be involve as indicators individual variability in movement patterns. Individual sampling was too low to obtain a clear effect at nesting sites level. However specific species pattern was clearly observed and variability between individual at each species level could suggest potential differential migration pattern. Thus, we suggest that the combination of the "microbial map" of the carapace biofilm of sea turtle and the "elemental signature" of their eggshells can open a new window onto their spatial and trophic ecology and could be useful tools for the management and conservation of these species.

Algae biofilm diversity and ecology

Our results demonstrated an important interspecific difference between biofilms developed on analysed turtle seashell species, with a sparse and poorly diversified biofilm in the leatherback comparatively to the hawksbill turtles. Chloroplast communities, associated with the hawksbill turtle, exhibit higher species richness (chao1), diversity (Shannon index), and evenness than those of the leatherback turtle. These differences are supported by the Wilcoxon signed-rank test, a non-parametric test that compares distributions between two groups, and by a Cliff's δ close to 1, indicating a very marked difference between the hawksbill and leatherback turtles. The R^2 values show that the species group factor explains a large part of the variability in richness and diversity. In contrast, the lack of a significant difference in Simpson's index (1–D) suggests that the dominance structure of taxa, i.e., the ratio of common to rare species, remains comparable between the hawksbill and leatherback turtles. Moreover, the rarefaction curves (**Fig. 3**) showed that OTU richness in leatherback turtles remains very low and led us to hypothesize that either our sampling effort of this species was insufficient or that it genuinely harbours a very low chloroplastic biofilm diversity. Consequently, the overall diversity pattern observed in our study appears to be primarily driven by hawksbill turtles. Only 16 OTUs were detected in samples of the leatherback turtles and identified to diatoms (Bacillariophyta) reflecting result of Robinson et al., (2016) showing a presence of epibiotic diatoms on all sea turtle species. The hawksbill turtle exhibited largely higher diversity (225 OTUs) and a much more pronounced enrichment of its carapace in algal taxa. The algal biofilm community was mostly dominated by diatoms (79.4% of OTUs), with a more limited amount of red, brown, and green macroalgae, as well as a few less abundant other microalgae groups. In terms of taxonomic assignation, only 17% of the OTUs could be clearly identified to the species level. Thus, 83% of the OTUs were identified only at the genus, family, or a higher taxonomic level. This proportion of unresolved identification to the species level is particularly pronounced among the Bacillariophyta, where 92.1% of the OTUs are not identified to the species level.

We observed a predominance of taxa known coupling pelagic and benthic life phases (pelagobenthic). Considering all 241 OTUs, approximately 72% were tentatively characterised as pelagobenthic, 13% as strictly pelagic, and 8% as benthic, while epibenthic taxa and OTUs of clearly terrestrial origin are respectively about 2.1% (see **Fig. 33** in Annexe V). This dominance of pelagobenthic taxa indicates that carapace biofilms provide a substrate for organisms exploiting both pelagic and benthic niches, shaped by host movement and by the hydrodynamic conditions created at the water-carapace boundary. OTUs associated with the leatherback align seamlessly with this pattern, consisting exclusively of pelagobenthic or cosmopolitan benthic diatoms. When restricting our habitat analysis to the 41 OTUs that reached a species level assignment, the habitat profiles are less pronounced. Although OTU retrieved were quite restricted for this species, with a less pronounced habitat profile. Among these OTUs, 31.7% were potentially associated to pelagic taxa, 26.8% as pelagobenthic, 24.4% as benthic, and 9.8% are epibenthic. Pelagic classified taxa were mainly planktonic diatoms (*e.g.*, *Arcocellulus mammifer* or *Attheya septentrionalis*), while the pelagobenthic category includes more tolerant taxa alternating between the water column and the microphytobenthos, such as *Cylindrotheca closterium*. Strictly benthic taxa include some red or brown macroalgae (*e.g.*, *Fucus vesiculosus* or *Palmaria palmata*), typically attached to hard substrates (Blanc et al., 2023; Stévant et al., 2023). Moreover, several OTUs were assigned to taxa typically linked with carbonate environments. These include the endolithic green alga *Ostreobium* (Ostreobiaceae; e.g. *Ostreobium quekettii*), a euendolithic symbiont that actively bores into and inhabits coral $CaCO_3$ skeletons (Verbruggen & Tribollet, 2011; Iha et al., 2021). They also include articulated coralline red algae in the Corallinales (e.g. *Calliarthron tuberculosum*), which typically lives on wave-exposed rocky shores (Donham et al., 2022). Their presence on turtle carapaces indicates that carapace biofilms can host photosynthetic taxa adapted to coral-associated endolithic niches as well as other specialised calcifying marine environments. Their presence could also be explained by the presence of debris or spores from these photosynthetic, often multicellular organisms. Finally, of these 41 taxonomically annotated OTUs, approximately 58.5% are classified as occasional epibionts and 12.2% as clearly epibionts, meaning that ~70.7% can at least occasionally colonise biological substrates (*e.g.*, benthic diatoms such as *Cylindrotheca closterium* or *Navicula* sp.). The remaining 29.3% correspond to non-epibionts, which are mostly here planktonic forms such as *Arcocellulus mammifer* or *Attheya septentrionalis*. However, this category of "strictly non-epibionts" should be interpreted with caution, as it also reflects the limitations of available ecological knowledge for some taxa retrieved and reported in Algaebase and Worms databases (Guiry & Guiry, 2024; WoRMS Editorial Board, 2025).

From all 41 taxa identified, 26.8% are associated with a cosmopolitan distribution in coastal and surface marine waters. The others exhibit varied regional distributions across temperate, polar, subtropical, and tropical zones. They include species found from temperate to tropical coastal environments, lagoons and salt marshes, as well as taxa linked to specific regions such as the Gulf of Mexico, each representing only a few percent of the identified species. Some taxa identified in the hawksbill turtle appear to originate from unexpected areas. Examples include *Calliarthron tuberculosum* in the Northeastern Pacific Coast (Gabrielson et al., 2011) and *Vitrella brassicaformis,* another photopsynthetic protist usually associated to coral reef system. stromatolites and other calcifying environments (Oborník et al., 2012). Other examples are *Fucus vesiculosus*, *Palmaria palmata*, *Arcocellulus mammifer*, and *Attheya septentrionalis*, which are primarily described in temperate to cold or subpolar waters (Guiry & Guiry, 2024). This small group of species suggests the limits of taxonomic assignment.

Overall, the combination of a strong dominance of diatoms, a majority of widely distributed OTUs, and a very high percentage of taxa with epibiont potential suggest that Caribbean Sea turtle carapaces function as “collectors” of various compartments of the coastal microflora (Majewska et al., 2015b; Robinson et al., 2016; Kaleli et al., 2020). Consistently, several molecular approaches show that the microbial communities associated with the carapaces are distinct from the surrounding environment and reflect the environmental history and behaviour of the host (Rivera et al., 2018). In this context, the marked contrast between leatherback and hawksbill is particularly revealing that leatherbacks host only a small subset of the flora (16 diatom OTUs), while hawksbills concentrate almost all the remaining diversity. These results agree with the pattern described by Riaux-Gobin et al. (2021), reporting a significantly higher diatom richness in the hawksbill than in the leatherback. However, leatherbacks studied by Riaux-Gobin et al. (2021) exhibited a distinct and less diverse diatom community, probably linked to their highly oceanic and diving lifestyle. Indeed, several authors suggest that the highly pelagic nature of the leatherbacks limits the diversity of its epizoic flora compared to turtles exploiting coastal and benthic habitats (Ashworth et al., 2022). On the other hand, the hawksbill is described as bearing highly diverse and locally structured epibiont communities (Loghmannia et al., 2021), with carapace bacterial communities distinct from those of inert substrates (Loghmannia et al., 2023). Several studies also confirm that hawksbill is among the turtle species hosting the richest diatom communities, with high geographic variability (Majewska et al., 2017; Riaux-Gobin et al., 2021).

Our biogeographic profiles, dominated by taxa with a cosmopolitan coastal distribution, align with the view proposed by Riaux-Gobin et *al*. (2021) suggesting that the carapaces hold a mix of common diatoms and, less often, potentially epizoic species that are from more restricted areas. While *Navicula dermochelycola sp*. is emblematic of leatherback-associated epizoic diatoms, this study does not foreground these taxa, in contrast to certain morphology-based investigations (Riaux-Gobin et al., 2020; Riaux-Gobin et al., 2021). This discrepancy, already highlighted by Rivera et al. (2018) and discussed by Riaux-Gobin et al. (2021), illustrates the current limitations of sequence databases for epizoic diatoms and the strong complementarity between morphological approaches and metabarcoding. Furthermore, in this study, the low proportion of OTUs identified down to the species level (~17%), especially from the *Bacillariophyta* Class, underscores the limitations of databases for this type of community and calls for caution in biogeographical interpretation, particularly for the few species that are not considered Caribbean and could result from uncertain assignments or an incomplete taxonomy. Conversely, some minority groups, such as *Compsopogonophyceae* (red algae) or *Ulvophyceae* (green algae) are represented only by OTUs identified to the species level, which illustrates a bias related to the availability of references and degree of taxonomic description of the different groups (Wangensteen et al., 2018; Jerney et al., 2023; Groussman et al., 2023). The use of additional markers (e.g., 18S) and, more broadly, shotgun metagenomic datasets, which are still rare compared to targeted metabarcoding (Majewska et al., 2017; Rivera et al., 2018), could help refine these inventories. A significant proportion of the detected OTUs could not be identified at a species level, indicating that they are potentially new sequences for science (Mann et al., 2010). These unidentified OTUs suggest that a large fraction of the epibiotic diversity of sea turtles remains unknown and could, for example, correspond to true specialized epibiotic diatoms (Robinson et al., 2016; Rivera et al., 2018; Riaux-Gobin et al., 2021). Regarding avenues for research to explore, the characterization of these OTUs seems relevant. A strategy combining isolation and culture of strains, conventional DNA sequencing (barcoding), and formal morphological description would allow for the development of reference databases (Rimet et al., 2019). Single-cell barcoding, applied after microscopic characterization, would also offer a robust way of directly linking a given morphotype to a unique sequence (Hamilton et al., 2015). All of this aims to contribute to the ongoing effort to establish reference databases.

Finally, the low epibiotic diversity and abundance observed on leatherbacks may be linked to their migration behaviour between cold-temperate foraging grounds in the North Atlantic and their tropical nesting sites, if these thermal shifts could promote increased skin turnover and partial loss of established biofilms. A comparable temperature-induced mechanism has been suggested for high-latitude whales, in which Antarctic killer whales move to warmer seas to molt and get rid of their diatom-rich biofilm they carry (Durban & Pitman, 2012; Pitman et al., 2019; NOAA Fisheries, 2020). This parallel reinforces the idea that large, mobile marine vertebrates, such as turtles and whales, act as dynamic substrates and ways for epibiotic diatoms and other biofilm bacteria to spread.

TMEs composition

TMEs analyses show interspecific differentiation in the trace metal composition of the eggshells and a lack of correlation between TMEs found in the sand and the eggshells. Indeed, the three beaches were clearly distinct and reflect their respective environments. Madiana, located in the heart of the city of Schœlcher, on the edge of Fort-de-France, was characterized by dark volcanic sand, enriched in metals typical of this context (Fe, Ti, Mn, V, Sb, Pb, Zn, etc.). Conversely, Salines beach was more remote, and composed of white sand of coral origin, where elements associated with carbonates (Na, Mg, Ca, Sr, U, etc.) predominate. Finally, Diamant beach presented an intermediate situation, both geographically and geochemically. However, despite these marked contrasts in sand composition, the elemental profiles of the eggshells did not reflect those of the beach sediments, suggesting limited element transfer between the sand and the eggshells. This result was consistent with some observations reported in the literature (Al-Musharafi et al., 2015; Simões et al., 2019; Tanabe et al., 2022), although other studies have reported significant correlations (Jian et al., 2021; Naghilou et al., 2025).

Regarding the interspecific differences we observed, the leatherback turtle eggshells concentrate several trace metals (Fe, V, As, Pb, Cd), suggesting a higher exposure to pollutants and a potential maternal transfer, which would be in agreement with previous work on TMEs in eggs, eggshells and adults in leatherbacks (Guirlet et al., 2008; du Preez et al., 2018; Guzman et al., 2020). Notably, liver concentration measurements in stranded leatherback turtles showed high levels of As, Cd, Pb, and Se (Caurant et al., 1999; Orós et al., 2021). Maternal transfer of certain TMEs has been clearly demonstrated in French Guiana, where the concentrations of Se and Cd in the blood of females are positively correlated with those measured in their eggs, while Pb is also detected in both matrices

(Guirlet et al., 2008). There is a consensus on oviparous vertebrates: the initial pollutant load in eggs (including the shell) originates primarily from maternal transfer during oogenesis (Ehsanpour et al., 2014). Concerning the hawksbill turtles, studies showed the presence of Cd, Cu, Zn, Pb, and Hg in the blood of females and in different egg fractions suggesting a maternal transfer (Ehsanpour et al., 2014; Ahmadi et al., 2024). It can be noted that for certain TMEs, the hawksbill turtle appears to have lower concentrations than other species of sea turtles (Ehsanpour et al., 2014; Macedo et al., 2015; Ahmadi et al., 2024). Studies suggest that the interspecific differences are attributed primarily to trophic ecology: the hawksbill turtle, with its more specialized diet and lower trophic level, bioaccumulates fewer metals than species like the leatherback, where biomagnification is more pronounced (Ehsanpour et al., 2014; Ahmadi et al., 2024). Comparable results have been obtained in the loggerhead sea turtle (*Caretta caretta*) in the Mediterranean, where the accumulation of metals in tissues and eggs is linked to dietary specialization and maternal transfer (Savoca et al., 2022).

Through maternal transfer, this separation could also be attributed to the diet. Indeed, leatherback turtles feed primarily on cnidarians, while the hawksbill turtles' diet is based on sea sponges. The literature shows that North Atlantic jellyfish accumulate a large range of trace metals. This has been shown through multiple studies, from the North Atlantic and the Mediterranean, and included Zn, Cu, Fe, Mn, As, Cd, and Pb contamination in the jellyfishes' tissues (Morais et al., 2009; Chouvelon et al., 2022; Raposo et al., 2022; Cruz et al., 2024). The fact that leatherback turtles were associated with these trace metals could be explained by a trophic intake dominated by jellyfish, while the lower profile of hawksbill turtles reflects a specific trophic ecology based on sponges. Indeed, the hawksbill turtle is a coral reef specialist, feeding primarily on sponges, with a taxonomically very restricted diet (approximately 95% of its diet consists of sponges in some areas; Meylan, 1988). Subsequent studies confirmed this diet dominated by benthic invertebrates (sponges, but also sometimes corals and other invertebrates) and a position at a relatively low trophic level in the reef system (Leon & Bjorndal, 2002; Obura et al., 2010). Studies of metal contamination in the hawksbill turtle were consistent with this trophic niche. The results obtained by Ehsanpour et al. (2014) and Ahmadi et al. (2024), showed that Cd, Zn, Pb, and Hg were detectable in the blood of adults and in different egg fractions, proving maternal transfer, but in lower concentrations compared to other sea turtle species. Ehsanpour et al. (2014) emphasize that the relatively low metal concentrations in blood were consistent with the species' predominantly low-trophic-level diet.

Thus, while leatherback turtles exhibit higher metallic signatures, consistent with a pelagic lifestyle and the consumption of jellyfish that are potential vectors of certain TMEs, the lower TMEs levels differentiation observed in hawksbill turtles could fit a diet dominated low-trophic-level prey, and a more coastal ecology. Even so, both species remain exposed to TMEs and can transfer them to their offspring.

Potential indicator of movement pattern

In both biofilm and TMEs composition, we observed an important individual variability within each species. Therefore, a larger-scale study incorporating physiological and environmental variables would allow us to assess the extent to which these tools can infer the presence or absence of similar migratory patterns, and thus account for the individual variations observed in this study. Indeed, Robinson et al., (2016) hypothesised that diatom composition may serve as a biogeographical indicator of the whereabouts of sea turtles, especially for species that host particularly diverse diatom communities. Therefore, by comparing the diatom flora on sea turtles with known marine benthic diatom floras worldwide, it may be possible to detect where the turtle has been residing (Rivera et al., 2018). Furthermore, with a larger-scale variables and samples, the potential existence of a link between biofilm composition and individual health status would require further research to assess whether the biofilm can be considered a potential microbiota.

3.7 CONCLUSION

This exploratory study highlighted the use of innovative and non-invasive techniques, such as the characterization of turtle shell biofilms using metagenomics and the quantification of metabolic waste products (MWPs) in the eggshells of two threatened sea turtle species. These two techniques provided an initial overview of these sea turtle populations in Martinique and highlighted potential biases and future research possibilities. The hypothesis that the taxonomic composition of biofilms reflects the ecological environments encountered by the hosts remains partially answered and warrants further investigation. Thus, to better understand the lack of eukaryotic diversity composing the leatherbacks biofilm and for comparison purposes, it would be interesting to analyse some samples from their feeding grounds in the Noth-Atlantic Sea. The same reasoning applies to the idea that metals accumulate in eggshells, reflecting the trophic exposure of females within their visited habitats Finally, this study retrieved an interspecific differentiation further supported using the 16S rRNA marker which allowed us exploring biofilm composition and phytoplankton diversity associated with the leatherback and hawksbill turtles of the Lesser Antilles.

CONCLUSION GÉNÉRALE

Les tortues marines sont de véritables ponts entre mer et terre. Bien qu'adaptées à la vie aquatique où elles passent 99% de leur vie, elles réalisent un acte crucial sur terre : la ponte de leurs œufs sur les plages de nombreux pays (Cayol, Maillard & Dubief, 2008). Par cet acte, elles enrichissent les sols en nutriments non-négligeables pour des zones souvent oligotrophes (Hannan et al., 2007). De plus, les tortues marines sont des espèces emblématiques et charismatiques qui permettent, de part cette notoriété, de protéger l'ensemble des écosystèmes qu'elles abritent (Gallegos-Fernández et al., 2023). Le travail effectué au cours de cette maitrise a fourni de nouvelles informations sur les populations de tortues luth et imbriquées en ponte sur trois plages de la Martinique, qui sert de laboratoire et de modèle reproductible pour d'autres territoires. Dans cette conclusion générale, nous aborderons les principales découvertes et résultats obtenus dans les trois chapitres qui compose cette thèse, ainsi que les perspectives et questions de recherches qui en découlent.

Le premier chapitre de cette étude a permis d'explorer l'impact d'un ouragan précoce de forte intensité sur les pontes de tortues luth et imbriquées. Nos observations ont mis en évidence la forte sensibilité des tortues luth aux ouragans précoces, dont la fréquence et l'intensité sont appelées à augmenter avec le réchauffement climatique. En effet, du fait de leur comportement de ponte, caractérisé par une nidification proche de la ligne d'eau, et de fenêtres de ponte plus courtes et concentrées en début de saison, les tortues luth apparaissent particulièrement vulnérables aux ouragans précoces, contrairement aux tortues imbriquées, qui semblent plus résilientes. Les résultats obtenus dans cette étude ont été combinés à ceux de deux autres tempêtes/ouragans dans une récente publication parue dans la revue *Le Climatoscope* (Langel et al., 2025b), qui met également en avant l'impact de ces événements climatiques sur l'érosion des côtes de nos sites d'études et la disparition des cordons sableux, susceptibles d'affecter à l'avenir les pontes de tortues marines. Poursuivre la documentation de l'impact de ces événements climatiques intenses est essentiel pour caractériser l'érosion à l'échelle locale, et, à terme, éclairer certaines observations récentes telles que la migration latitudinale de certaines zones de ponte des tortues marines (Patrício et al., 2021; Arora & Phillott, 2023) qui pourraient traduire une résilience des populations de tortues marines à travers le monde.

Le second chapitre de ce mémoire traitait de l'utilisation de la photoID dans le cadre des suivis de ponte annuel. Il a permis de mettre en avant des patrons comportementaux bien différentiés entre la tortue luth et la tortue imbriquée, avec la caractérisation de zones de ponte de prédilection. Nous avons pu démontrer les biais dans les méthodes classiques d'estimation des populations de tortues marines. En effet, les suivis classiques, basés sur le comptage nocturne des femelles en ponte, peuvent surestimer les effectifs en confondant remigrantes et premières pondeuses : ainsi, 61 % des tortues luth observées sur les trois plages étudiées en Martinique avaient déjà été photographiées au cours de la même saison. La photoID permettra, à terme, de reconnaître individuellement les femelles, mais aussi d'intégrer les mâles, les individus des îles voisines et les tortues luth migrant plus au nord, tout en révélant des préférences de microhabitats utiles à la restauration, comme chez l'imbriquée. Dans ce contexte, le développement de bases de données de photoID à l'échelle régionale ou mondiale est une priorité. Un projet de photoID des tortues luth de l'Atlantique Nord-Ouest, présenté en annexe, vise déjà à comparer ces populations à celles de la Caraïbe. Renforcer ce type de bases via des partenariats permettrait de mieux relier sites de ponte et zones d'alimentation et d'optimiser les stratégies de conservation (Annexe VI). Enfin, ce travail met en évidence, pour la première fois à notre connaissance, que les tortues imbriquées tendent à émerger de l'eau pour nicher dans une fenêtre horaire particulièrement restreinte à l'échelle de l'individu. Bien que le nombre d'observations reste limité, cette régularité temporelle ouvre des perspectives de recherche importantes. En finalité, elle pourrait influencer l'organisation des suivis nocturnes, affiner les estimations de population et aider à mieux comprendre la sensibilité de l'espèce aux dérangements anthropiques (lumière, bruit, fréquentation).

Enfin, le dernier chapitre a permis d'explorer le potentiel de nouveaux outils non-invasifs que sont l'analyse métagénomique du biofilm des carapaces des tortues rencontrées et l'analyse des éléments traces métalliques des coquilles vides. L'hypothèse étant que la structure microbienne du biofilm et le profil métallique des coquilles pouvaient conserver la trace des environnements traversés par les femelles au cours de leurs migrations alimentaires, et ainsi constituer des indicateurs indirects de leurs trajectoires. Ce chapitre a contribué au développement et à la validation de protocoles méthodologiques, confirmant la faisabilité de ces approches. Les analyses ont notamment révélé la quasi-absence d'eucaryotes chloroplastiques dans le biofilm des tortues luth et a mis en évidence une contamination en métaux traces potentiellement plus élevée chez cette espèce que chez la tortue imbriquée, en cohérence avec leurs différences écologiques et trophiques. Ces premiers résultats confirment l'intérêt de ces marqueurs microbiens et géochimiques pour mieux comprendre ces espèces, et ouvrent la voie à une lecture plus fine de l'hétérogénéité des trajectoires migratoires. De plus, l'analyse métagénomique du biofilm à partir du primer 16S et de la librairie PR2 a permis de constituer une base de données de taxons procaryotes. Ces données, qui feront l'objet d'un article ultérieur, permettront d'éclairer les liens entre les organismes eucaryotes étudiés au chapitre 3 et les communautés procaryotes, ainsi que de caractériser l'ensemble du biofilm. Au-delà de leur intérêt pour la biologie des migrations, ces outils soulèvent des questions essentielles quant à la santé des tortues marines, en particulier le lien entre composition du biofilm et l'état physiologique des individus. L'exploitation de ce potentiel bioindicateur nécessiterait d'augmenter le nombre d'échantillons, de diversifier les sites d'étude, et de déterminer l'état de santé de la tortue par des méthodologies plus invasives (e.g. biopsie ou prise de sang). De plus, l'analyse du biofilm des tortues luth en alimentation dans les eaux plus tempérées, comme dans le golfe du Saint-Laurent, permettrait de mieux comprendre la faible diversité eucaryotique retrouvée sur les femelles en ponte en Martinique et de valider l'hypothèse d'une perte de ces organismes dû aux changements de températures de l'eau. À terme, l'intégration du biofilm et des coquilles d'œufs dans un cadre de suivi à large échelle pourrait contribuer à mieux comprendre la réponse des populations de tortues marines aux pressions environnementales actuelles et futures, et à orienter plus efficacement les stratégies de conservation.

Dans l'ensemble, le suivi intégré des tortues luth et imbriquées des trois principaux sites de ponte de Martinique met en évidence à la fois la forte vulnérabilité de la tortue luth aux aléas climatiques extrêmes, l'importance de l'environnement et de l'activité humaine sur le comportement de ponte, et la pertinence d'outils innovants (photoID, métagénomique, métaux traces) pour caractériser les individus et les différences interspécifiques. Ces résultats positionnent la Martinique comme un observatoire pilote, dont le schéma de suivi est transposable à d'autres territoires et d'autres espèces de tortues marines.

Pour conclure, on peut rappeler que les tortues marines appartiennent à un clade apparu au Trias tardif (~230 Ma) et dont la morphologie générale a traversé au moins deux grandes extinctions de masse : l'extinction de fin-Trias (~201 Ma) et celle du Crétacé–Paléogène (66 Ma) sans les faire disparaître, démontrant leur résilience (Pérez-García, 2020; Hermanson & Evers, 2024; Liaw et al., 2025).

ANNEXES

ANNEXE I

Analytical Precision and Sample Heterogeneity in eggshells Trace Metal Elements

We evaluated the analytical precision, on four eggshells samples analysed in duplicate, using the Relative Percentage Difference (RPD%). Considering the five most significant and present elements, the results are of acceptable quality for P (8.5% [0.4–44.1]) and Mg (10.3% [4.1–26.2]). Ca remains more variable (15.1% [7.7–58.1]), while Fe shows moderate dispersion (17.6% [5.5–27.3]) and Sr the highest (23.5% [12.3–67.1]). The Relative Standard Deviation percentage (RSD%) of the samples and replica are, respectively: Ca 68.9% and 86.3%; Mg 45.3% and 40.5%; P 71.9% and 59.6%; Fe 141.1% and 151.4%; Sr 68.1% and 61.3%. This indicates significant variability and some heterogeneity between samples.

ANNEXE II

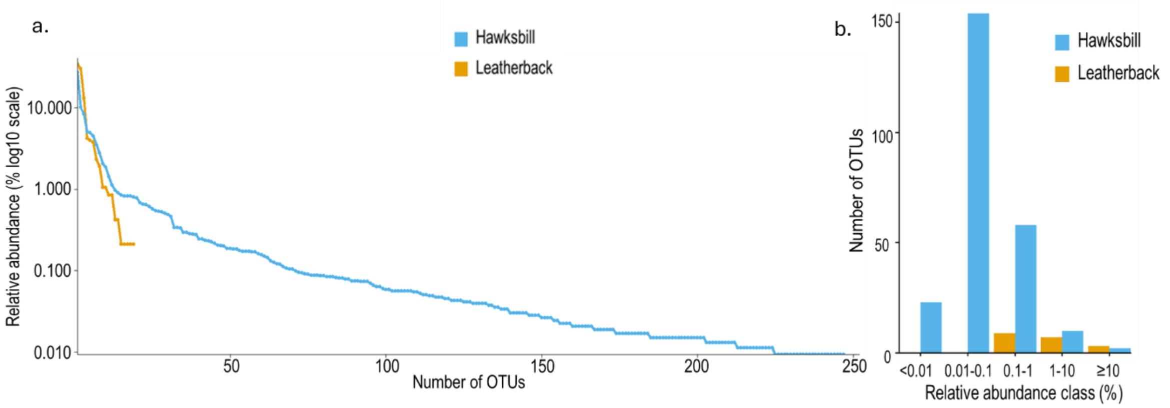

Figure 30. Comparison of community structure between hawksbill (blue) and leatherback (orange). (a) Rank-abundance curves and (b) distribution of eukaryotic OTUs by abundance classes.

The rank-abundance curve (a) shows, for each turtle species, the relative frequency of all detected OTUs, ranked in descending order of abundance (hawksbill in blue, leatherback in orange). The length of the curve reflects the richness of OTUs, while the slope indicates the evenness of the community. The bar chart (b) presents, for the same data, the number of OTUs per abundance class, allowing us to distinguish the proportion of rare, intermediate, and dominant OTUs in each species. Together, these two representations show that the hawksbill community is richer and includes a greater proportion of rare OTUs than the leatherback community.

ANNEXE III

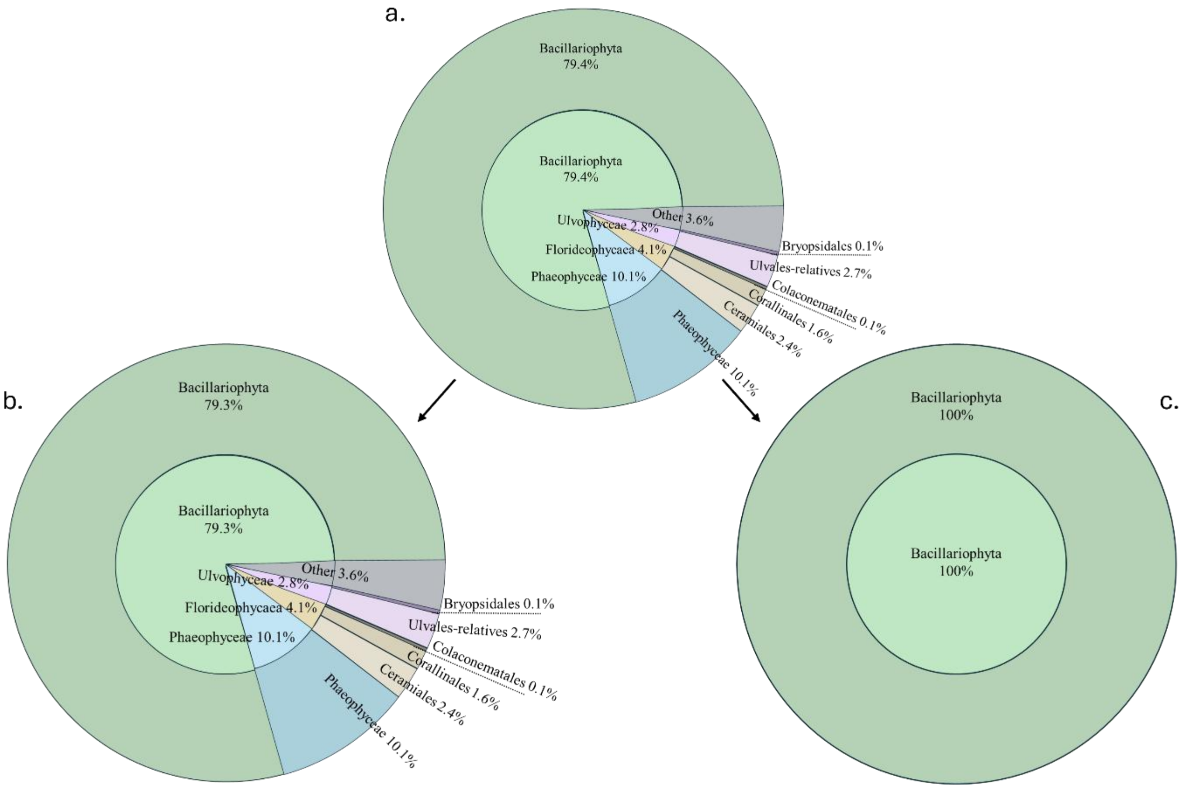

Figure 31. Taxonomic composition of plastidial biofilms. (a) hawksbill and leatherback composition (b) hawksbill (*Eretmochelys imbricata*) samples only, (c) leatherback (*Dermochelys coriacea*) samples only. The central disc represents the Class, while the outer ring details the composition at the Order level.

ANNEXE IV

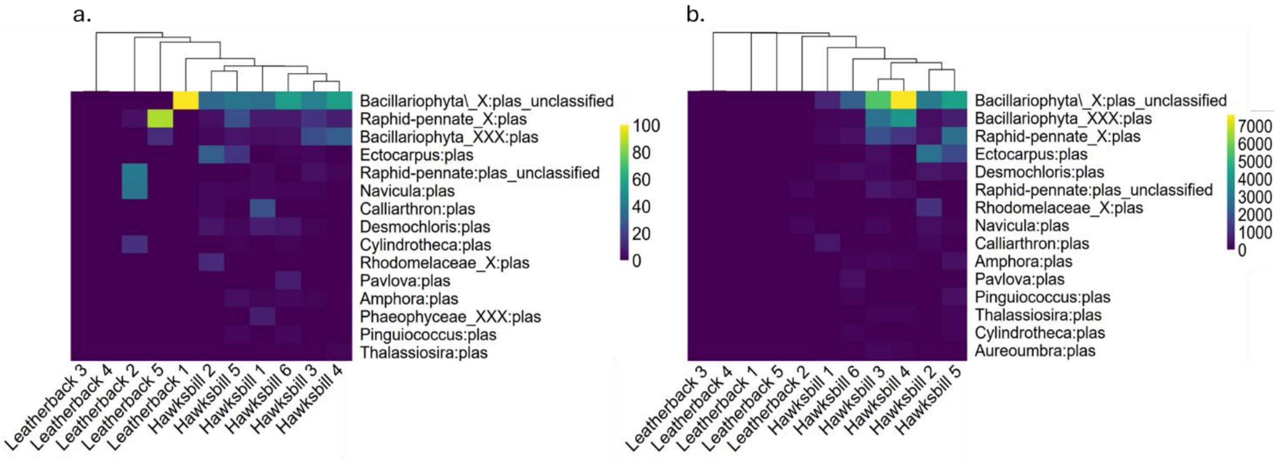

Figure 32. Heatmap of relative abundances and clustering of eukaryotic genera in hawksbills (*Eretmochelys imbricata*) and leatherback (*Dermochelys coriacea*) samples. Colour intensity indicates relative proportion per taxon and per sample in relative abundance (%; a) and total OTU (b).

ANNEXE V

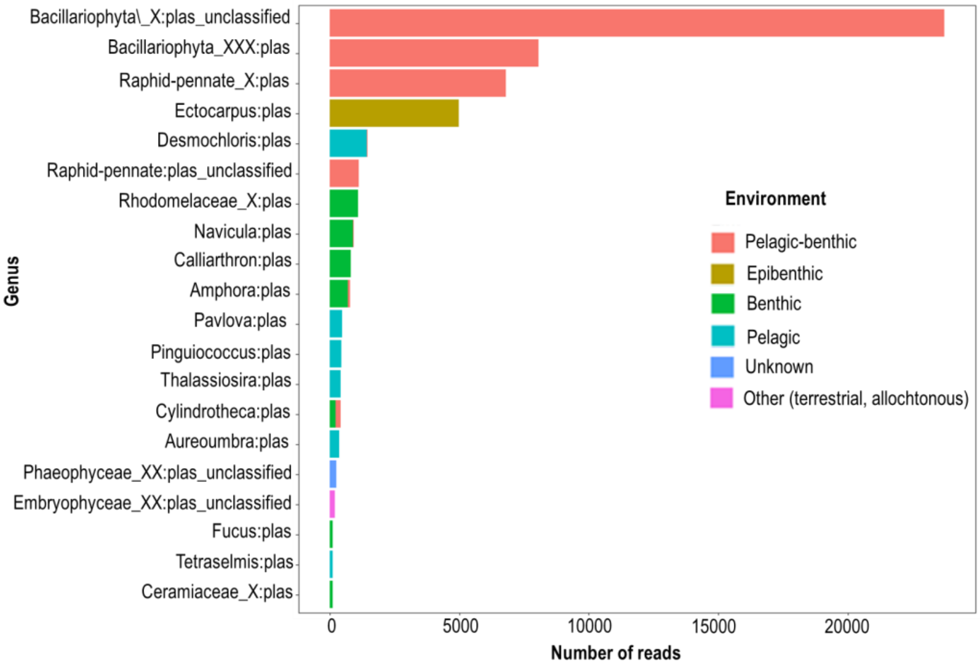

Figure 33. Distribution of the main genera according to their environmental affinity.

Total number of reads assigned to the main genera identified by metabarcoding, ranked in descending order of abundance. The colors indicate the environmental affinity of each genus (pelagic, benthic, pelagic-benthic, epibenthic, other or unknown), showing the strong dominance of diatom taxa (*Bacillariophyta_X*, *Bacillariophyta_XXX*, *Raphid-pennate_X*) mainly associated with pelagic-benthic habitats.

ANNEXE VI

Identification photographique des tortues luth (*Dermochelys coriacea*) entre la Martinique et l'Atlantique Nord-Ouest

Introduction

La tortue luth (*Dermochelys coriacea*) est une espèce menacée, tout au long de sa vie, par de nombreux facteurs, tels que la pêche accidentelle ou la dégradation de son habitat (Cook, 1981; COSEPAC, 2001; Spotila et al., 2000; Wallace et al., 2011). Un suivi efficace de l'espèce est essentiel pour comprendre les mouvements et les dynamiques des populations, notamment entre leurs sites de ponte majeurs, comme les Antilles, et leurs zones d'alimentation en Atlantique Nord. Les méthodes de traçage traditionnelles, tel que le bagage, Pit Tag ou les balises GPS, même si généralement efficaces, restent coûteuses et invasives (Balazs, 1999; Eckert & Eckert, 1990; Buonantony, 2008). De plus, les balises satellitaires ou le bagage métallique tendent à tomber avec le temps et a facilité l'implantation d'espèces épibiontes, tels que les balanes (*Chelonibia lepas*) défavorisant les individus marqués (Limpus et al., 1992; Parmenter, 1993; Bjorndal et al., 1996). Enfin, les balises satellitaires altèrent l'hydrodynamisme des tortues marines (Watson & Granger, 1998; Jones et al. 2011a). La photo-identification (PhotoID) semble être une approche universelle, permettant de pallier les problématiques observées lors de l'utilisation des méthodes habituelles. En effet, cette technique à un coût extrêmement faible, peu invasive, la photo pouvant être prise à distance, en plus d'être accessible à tous, permettant le développement de projets de sciences participative (Buonantony, 2008; Hof et al., 2017; Hendrix & Pérez-Espona, 2024; Phillott & Yaghmour, 2024). Aucune base de données n'est officiellement utilisée en Atlantique. Ce projet a pour objectif de développer une base de données de photoID, basée sur la morphologie unique de la tache pinéale, une marque distinctive présente sur le dessus de la tête des tortues luth (McDonald & Dutton, 1996). En créant un catalogue de profils individuels, l'étude cherche à établir une méthode fiable et non-invasive pour identifier les tortues dans différentes régions, en commençant par une île des Caraïbes, la Martinique, le golfe du Saint-Laurent ainsi que les eaux de Saint-Pierre-et-Miquelon.

Matériel et Méthodes

Site d'étude

Les photographies collectées proviennent de l'Atlantique Nord-Ouest, plus précisément de l'Est du golfe Saint-Laurent, du large de la Nouvelle-Écosse et de Saint-Pierre-et-Miquelon, où les tortues luth se nourrissent et migrent abondamment (Fossette et al., 2010; Dodge et al., 2014), ainsi que sur trois plages de nidification de la Martinique, un site clé pour la reproduction dans la région (**Fig. 33**; Delcroix et al., 2014).

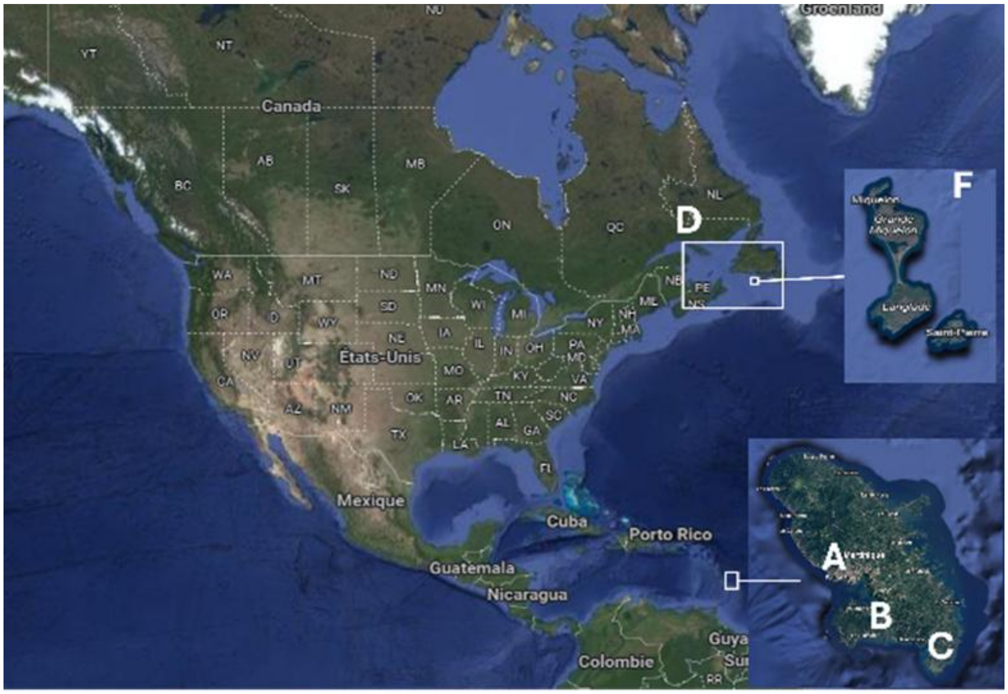

Figure 34. Carte des zones où les tortues luth ont été photographiées : la Martinique avec trois sites de ponte, Madiana (A), Diamant (B) et les Salines (C); le golfe du Saint-Laurent (D) et Saint-Pierre-et-Miquelon (F).

Collecte des données

Les photographies de l'Atlantique Nord-Ouest proviennent de l'organisme Sea Turtle Canada Network, collectées dans le cadre de leurs suivis annuels (2006–2023). En complément, un groupe de quatre photographes de Saint-Pierre-et-Miquelon a contribué activement à la base de données en fournissant des clichés pris entre 2005 et 2024. Les photographies des trois sites de ponte en Martinique sont issues de quatre années de suivis nocturnes (~avril–octobre; 2021, 2023–2025), au cours desquelles chaque femelle aperçue a été photographiée conformément au protocole établi.

L'ensemble des données et photos sont disponibles sur le serveur d'Aquasearch sur demande.

Analyses

Les photos ont toutes été analysées à l'aide du logiciel I3SPattern v3.0 (Interactive Individual Identification System, ©2020 Reijns/i3s) pour l'identification individuelle des tortues, méthode reconnue pour son efficacité et sa fiabilité (Speed et al., 2007; Van Tienhoven et al., 2007; Den Hartog & Reijns, 2012; Steinmetz et al., 2018). Sa performance dépend toutefois de la qualité des images et de l'expérience des utilisateurs (Dunbar et al., 2014; Calmanovici et al., 2018; Steinmetz et al., 2018). Afin de réduire ces biais, des protocoles standardisés de prise de vue et d'analyse ont été appliqués. Trois points d'ancrage ont été définis sur la tache pinéale pour une standardisation de l'analyse I3S (Den Hartog & Reijns, 2014). Le logiciel compare ensuite 35 points de références et attribue un score de correspondance, mais une vérification manuelle reste indispensable (Dunbar et al., 2014). Enfin, un double contrôle a été réalisé par une autre personne pour limiter les biais d'observateurs et garantir la fiabilité des résultats. Les individus ainsi identifiés ont été comparés entre deux sites d'études (Saint-Pierre-et-Miquelon et Martinique) pour valider de potentielles migrations individuelles.

Résultats

Un total de 717 photographies a été reçu. Cependant, après un tri rigoureux fondé sur la qualité des clichés et la visibilité de la tache pinéale, seules 178 ont pu être retenues et analysées avec I3Spattern. Les photos utilisées provenaient du Canadian Sea Turtle Network (n = 45), de Saint-Pierre-et-Miquelon (n = 32) et d'Aquasearch (n = 101). Aucune correspondance d'individus n'a été détectée entre Saint-Pierre-et-Miquelon et la Martinique lors de cette première analyse ne permettant pas de confirmer la migration d'individus entre les deux sites.

Discussion

L'écart entre le nombre de photographies reçues et celui des photographies analysées s'explique principalement par une qualité insuffisante des clichés, ou par l'absence de vue nette de la tache pinéale. En mer, comme à Saint-Pierre-et-Miquelon, l'approche des tortues est souvent limitée, ce qui conduit à des photos prises à distance et/ou sous des angles ne permettant pas toujours d'observer correctement cette marque. L'absence de correspondance dans cette première analyse peut également s'expliquer par le faible effectif de photographies disponibles. On peut donc raisonnablement s'attendre à de meilleurs résultats lorsque le nombre de clichés sera plus élevé et que l'échantillonnage couvrira potentiellement des zones géographiques plus étendues.

Au-delà de l'avancement des connaissances scientifiques, cette approche a des implications majeures pour la conservation. Elle offre un outil de suivi économique et à faible impact, utilisable par les chercheurs et les acteurs de la conservation du monde entier (Schofield et al., 2008). À terme, le projet vise à contribuer à la protection durable des tortues luth grâce à des stratégies de gestion et de conservation mieux informées (Wallace et al., 2011). La combinaison des données d'observations en mer et des données de nidification nous permettra d'examiner la connectivité entre les zones de recherche de nourriture et de reproduction, d'améliorer les estimations de la taille des populations et de suivre la fidélité des femelles nicheuses au site (James et al., 2005c; Rivalan et al., 2006).

Remerciements

Ce projet n’aurait pu voir le jour sans l’engagement des photographes de Saint-Pierre-et-Miquelon : Frank Urtizberea, Joël Detcheverry et Thierry Vogenstahl. Nous remercions également l’équipe d’Aquasearch ainsi que leurs stagiaires pour le travail accompli, les nombreuses heures de suivi et la collecte des photos de tortues luth depuis 2020. Merci également à Sea Turtle Canada Network pour leurs collaborations. Enfin, merci à Camille Ngothe pour son aide sur le traitement des photos.

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