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Distribution et comportement de plongée des tortues marines de Guyane française sous l'influence des structures océanographiques

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À mes grands-parents,
Jacqueline et André Chambault

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Avant-propos

Démarrée en juin 2014, cette thèse s'inscrit dans le projet ANTIDOT (*Association of News Tools to Improve the understanding of the Dynamic Of threatened marine Turtles*). Initié en 2012, ce projet s'est focalisé sur les tortues marines de l'Atlantique occidental à différentes échelles spatio-temporelles, en étudiant leurs réponses aux turbulences océaniques, les tendances de leurs populations actuelles, ainsi que leurs comportements individuels de plongée et de migration. Pour remplir cet objectif, une série d'approches ont été utilisées : de (1) la génomique, qui doit identifier les réponses adaptatives des populations à l'évolution des conditions océanographiques du Pléistocène-Holocène, à (2) la CMR (Capture-Marquage-Recapture) sur les colonies de nidification, qui doit fournir une base biologique principale des processus de reproduction actuels, en passant par (3) le suivi en mer des individus, couplés à la description de leur habitat océanographique, afin de comprendre comment les tortues marines optimisent leurs ressources lors de la migration et durant la période de reproduction. C'est donc au sein de ce dernier axe que s'inscrit ce travail de thèse. L'obtention d'un financement de la part de Shell Guyane, du CNES Guyane, de la Mission pour l'Interdisciplinarité (CNRS), de la Fondation EDF, de la Fondation de France et du projet CARET2, pour étudier les *déplacements et le comportement de plongée des tortues marines de Guyane française sous l'influence des structures océanographiques* a permis la mise en place de nombreuses collaborations (le CEFE de Montpellier, le CEBC de Chizé, le LOCEAN de Paris, le MISU de Stockholm et CLS de Toulouse), qui ont abouti au document présenté ci-après.

Sigles et abréviations

AEM : Action d'État en mer
ANTIDOT : Association of News Tools to Improve the understanding of the Dynamic Of threatened marine Turtles
ARS : Area-Restricted Search
CCL : Curved carapace length
CCW : Curved carapace width
CEBC : Centre d'Études Biologiques de Chizé
CEFE : Centre d'Écologie Fonctionnelle et Évolutive
CLS : Collecte Localisation Satellite
CHL : Concentration en chlorophylle *a*
CMR : Capture-Marquage-Recapture
CNES : Centre National des Études Spatiales
CTD-Fluo : Conductivity-Time-Depth-Fluorescence
EST : Extented Surface Interval
FPT : First Passage Time
FSLE : Finite-Size Lyapunov Exponents
GPS : Global Positioning System
GEBCO : General Bathymetric Chart of the Oceans
HYCOM : HYbrid Coordinate Ocean Model
Kd : Coefficient d'atténuation de la lumière
LOCEAN : Laboratoire d'Océanographie et du Climat : Expérimentations et Approches Numériques
MIBE : Métrologie et Instrumentation en Biologie et Environnement
MKN : Micronecton
MISU : Meteorologiska Institutionen Stockholms Universitet
MLD : Mixed layer depth
MODIS : Moderate Resolution Imaging Spectroradiometer
NBC : North Brazil Current
PIT : Passive Integrated Transponder

PNA : Plan National d’Actions
PTT : Platform Terminal Transmitter
RFID : Radio frequency identification
RMU : Regional Management Units
ROV : Remotely operated vehicle
RT : Residence Time
SD : Standard Deviation
SE : Standard Error
SEAPODYM : Spatial Ecosystem And POpulation DYnamics Model
SMPE : Services Mixtes de la Police de l’Environnement
SMRU : Sea Mammal Research Unit
SRDL : Satellite Relay Data Logger
SSH : Sea Surface Height
SST : Sea Surface Temperature
TAD : Time Allocation at Depth
TED : Turtle Excluder Device
TTED : Trash and Turtle Excluder Device
UICN : Union Internationale pour la Conservation de la Nature
VGPM : Vertically Generalised Production Model
VHF : Very high frequency
ZEE : Zone exclusive économique
ZEU : Euphotic depth

Publications

Annexe	Chapitre	Article	Statut
A	3	**P. Chambault**, B. de Thoisy, L. Kelle, R. Berzins, M. Bonola, H. Delvaux, Y. Le Maho, D. Chevallier. (2016) Inter-nesting behavioral adjustments of green turtles to an estuarine habitat in French Guiana. *Marine Ecology Progress Series*. (555). 235-248.	Publié
B	4	**P. Chambault**, L. Giraudou, B. de Thoisy, M. Bonola, L. Kelle, V. Dos reis, F. Blanchard, Y. Le Maho, D. Chevallier. (2016) Habitat use and diving behaviour of gravid olive ridley sea turtles under riverine conditions in French Guiana. *Journal of Marine Systems*. (165). 115-123.	Publié
D	5	M. Baudouin, B. de Thoisy, **P. Chambault**, R. Berzins, M. Entraygues, L. Kelle, A. Turny, Y. Le Maho, D. Chevallier. (2015) Identification of key marine areas for conservation based on satellite tracking of post-nesting migrating green turtles (*Chelonia mydas*). *Biological Conservation*. (184). 36-41.	Publié
E	5	**P. Chambault**, D. Pinaud, V. Vantrepotte, L. Kelle, M. Entraygues, C. Guinet, R. Berzins, K. Bilo, B. de Thoisy, Y. Le Maho, D. Chevallier. (2015) Dispersal and diving adjustments of the green turtle *Chelonia mydas* in response to dynamic environmental conditions during post-nesting migration. *PLoS ONE*. 10(9).	Publié
F	5	**P. Chambault**, B. de Thoisy, K. Heerah, A. Conchon, S. Barrioz, V. Dos Reis, R. Berzins, L. Kelle, B. Picard, F. Roquet, Y. Le Maho, D. Chevallier. (2016) The influence of oceanographic features on the foraging behavior of the olive ridley sea turtle *Lepidochelys olivacea* along the Guiana coast. *Progress in Oceanography*. (142). 58-71.	Publié

G	6	**P. Chambault**, F. Roquet, S. Benhamou, A. Baudena, E. Pauthenet, B. de Thoisy, R. Crasson, M. Brucker, M. Bonola, V. Dos Reis, Y. Le Maho, D. Chevallier. (2017) The Gulf Stream frontal system : A key oceanographic feature in the habitat selection of the leatherback turtle ? *Deep-Sea Research Part 1*. (123). 35-47.	Publié
H	7	**P. Chambault**, C. Barnerias, D. Étienne, J. Gresser, B. de Thoisy, B. Guillemot, É. Dumont-Dayot, S. Régis, N. Lecerf, R. Bordes, Laurent Thieulle, F. Védie, J. Mailles, Y. Le Maho, O. Petit, D. Chevallier. Multidirectional migratory routes of immature green turtles reveal connecting paths between juvenile and adult habitats.	En préparation
I	7	M. Nivière, **P. Chambault**, É. Dumont-Dayot, Y. Le Maho, D. Chevallier. Residency and migratory patterns of juvenile and adult hawksbill turtles across the Caribbean.	En préparation

Conférences & formations

Conférences

- **P. Chambault**. Sur les traces des tortues marines de Guyane française. Conférence du Jardin des Sciences. 15 décembre 2016. Université de Strasbourg. Strasbourg-France. Oral.
- **P. Chambault**, Y. Le Maho, D. Chevallier. Distribution et comportement de plongée des tortues marines de Guyane française suivies par Argos. Conférence Argos. 6 octobre 2016. Collecte Localisation Satellite. Toulouse-France. Oral.
- **P. Chambault**. Concours 'Ma Thèse en 180 secondes'. Finaliste régionale (1^{er} prix du jury). Institut des Sciences et de l'Ingénierie Supramoléculaire. 24 mars 2016. Strasbourg-France. Oral.
- **P. Chambault**, Y. Le Maho, D. Chevallier. Influence des processus méso-échelle sur les déplacements des tortues marines de Guyane française. 24-28 novembre 2015. Cayenne-Guyane française. Oral.
- **P. Chambault**, B. de Thoisy, K. Heerah, A. Conchon, S. Barrioz, V. Dos Reis, R. Berzins, L. Kelle, B. Picard, F. Roquet, Y. Le Maho, D. Chevallier. The influence of oceanographic features on the foraging behavior of the olive ridley sea turtle *Lepidochelys olivacea* along the Guiana coast. 36^{th} Annual symposium on sea turtle biology and conservation. 01-04 mars 2016. Lima-Pérou. Oral.
- **P. Chambault**, C. Barnerias, É. Dumont-Dayot, Y. Le Maho, D. Chevallier. Developmental habitat and migratory pathways : identifying key areas to protect future breeding green turtles across the Caribbean-Atlantic region. 36^{th} Annual symposium on sea turtle biology and conservation. 01-04 mars 2016. Lima-Pérou. Poster. 1^{er} prix du meilleur poster dans la catégorie Conservation.
- **P. Chambault**, B. de Thoisy, D. Pinaud, V. Vantrepotte, L. Kelle, M. Entraygues, C. Guinet, R. Berzins, K. Bilo, Y. Le Maho, D. Chevallier. Dispersal and diving

adjustments of green turtles in response to dynamic environmental conditions during post-nesting migration. 11^{th} Ecology & Behaviour meeting. 18-21 mai 2015. Toulouse-France. Oral.

- **P. Chambault**, D. Pinaud, V. Vantrepotte, L. Kelle, M. Entraygues, C. Guinet, R. Berzins, K. Bilo, B. de Thoisy, Y. Le Maho, D. Chevallier. Post-nesting migration of green turtles to their foraging grounds : Dispersal and diving adjustments in response to dynamic environmental conditions. 35^{th} Annual symposium on sea turtle biology and conservation. 18-24 avril 2015. Dalaman-Turquie. Oral.

Formations

- Concours ’Ma Thèse en 180 secondes’ à l’Institut des Sciences et de l’Ingénierie Supramoléculaire de Strasbourg en mars 2016.
- ’Gestion du trac’ au Collège Doctoral européen de Strasbourg en mars 2016.
- ’Effective writting’ au Collège Doctoral européen de Strasbourg en octobre 2016.
- ’Prise de parole en public’ à l’Institut Pluridisciplinaire Hubert Curien à Strasbourg en septembre 2015.
- ’Marquage et pose de balises Argos sur des tortues marines’ en Martinique en juin 2015.
- ’Traitement et utilisation de données spatio-temporelles issues d’observations satellitaires et de modèles numériques d’océan allant de la physique aux écosystèmes’, à Collecte Localisation Satellite à Toulouse en févier 2015.

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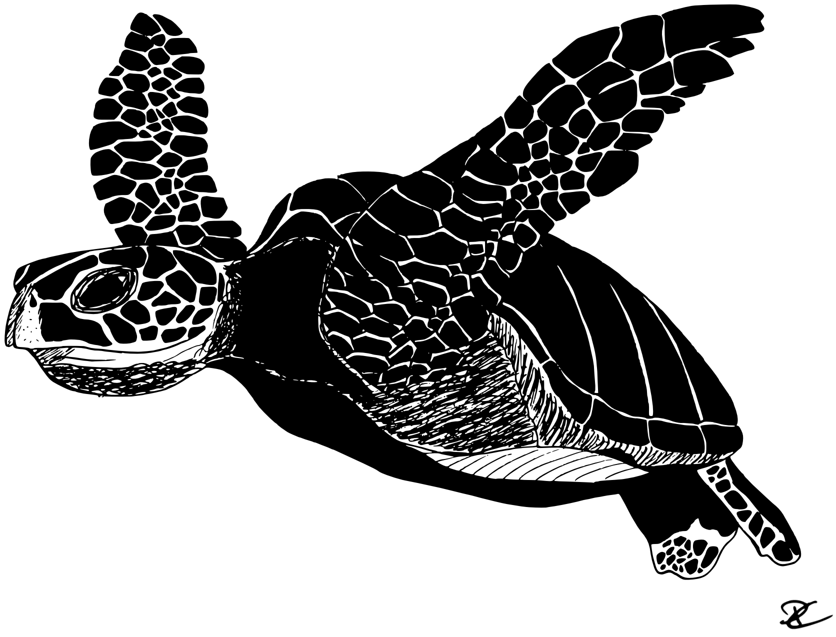
CHAPITRE 1

Introduction générale

Sommaire



1.1 L'océan : un écosystème hétérogène

De par son immensité et sa perpétuelle interaction avec l'atmosphère, l'océan est un environnement hétérogène et fortement dynamique qui s'organise autour de différents niveaux spatio-temporels (Hunt & Schneider, 1987). Sous l'influence d'une multitude de processus physico-chimiques, l'écosystème marin est en effet caractérisé par une importante variabilité causée par de complexes structures océanographiques à différentes échelles de temps et d'espace dans les trois dimensions (Barry & Dayton, 1991).

1.1.1 Variabilité horizontale

Cette variabilité se traduit tout d'abord par une forte hétérogénéité spatiale, opérant dans la couche supérieure de la colonne d'eau, et se traduisant par différentes structures océanographiques, à commencer par les structures à large échelle.

La méga-échelle : les gyres océaniques et courants principaux

À l'échelle des grands bassins océaniques (Atlantique nord, Atlantique sud, Pacifique nord, Pacifique sud et Indien), l'océan circule sur des milliers de kilomètres entre les différents continents, formant de gigantesques tourbillons d'eau : les gyres océaniques (gyres subpolaires et subtropicaux, Williams & Follows 2011) - Figure 1.1. Façonnés par la circulation des vents, ces gyres circulent dans le sens des aiguilles d'une montre dans les régions tropicales de l'hémisphère nord et dans le sens inverse dans l'hémisphère sud. Dans les plus hautes latitudes, leur sens de rotation s'inverse. Sur la façade occidentale de chaque bassin océanique on distingue de puissants courants tels que le Gulf Stream et le courant nord-brésilien dans l'Atlantique nord, ou encore le courant Kuroshio dans le Pacifique nord.

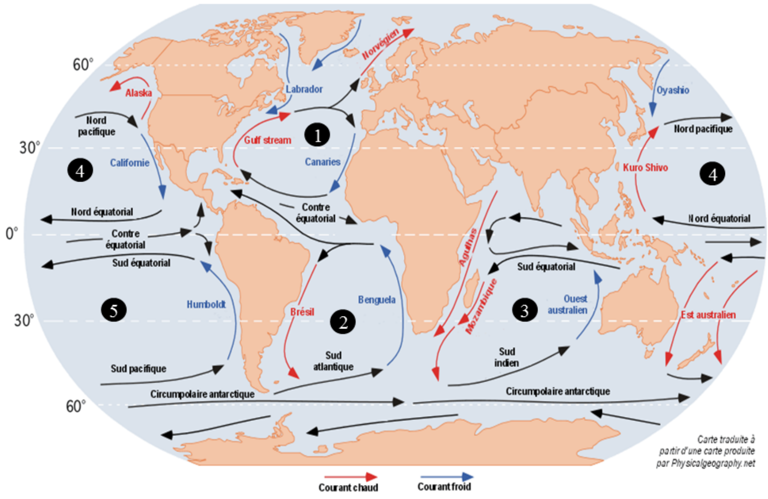


FIGURE 1.1 – Circulation océanique générale. Les numéros font référence aux différents gyres océaniques. Carte extraite de PhysicalGeography.net.

La macro-échelle : les masses d'eau

Le déplacement des masses d'eaux de surface associées aux courants marins va permettre le transport des nutriments dans les différents océans du globe. Les principaux facteurs générant le déplacement de ces masses d'eau sont (1) les vents, qui influencent la direction des courants dans la couche supérieure de la colonne d'eau (2) et les gradients de pression, causés par les différences de densités de l'eau ou de hauteur d'eau en surface (Ganachaud *et al.*, 2011). En complément, la force de Coriolis influe sur la direction des courants en raison de la rotation de la Terre, déviant ainsi vers la droite les eaux situées dans l'hémisphère nord, et vers la gauche celles situées dans l'hémisphère sud (Ganachaud *et al.*, 2011).

La méso-échelle : les tourbillons et fronts océaniques

Cette circulation océanique complexe génère par endroits des zones tourbillonnaires sous l'influence de processus de convergence comme c'est le cas le long du Gulf Stream (Ducet *et al.*, 2000; Lozier *et al.*, 1995; Schmitz & McCartney, 1993), ou encore le long du plateau des Guyanes, *e.g.* région de la côte nord-est de l'Amérique latine s'étendant du Guyana au nord du brésil délimité par l'Amazone (Didden & Schott, 1993). Ces tourbillons peuvent s'étendre sur des centaines de kilomètres et se maintenir pendant plusieurs semaines, voire plusieurs mois, avant de se dissiper. De telles structures entraînent l'augmentation de la production primaire et secondaire *i.e.* soit la production de matière vivante à partir de nutriments minéraux, d'eau et d'une source d'énergie (Olson *et al.*, 1994; Olson & Backus, 1985). Au sein d'un écosystème, les organismes se positionnent à différents niveaux de la chaîne trophique, permettant ainsi l'échange de biomasse et d'énergie dans l'intégralité de la chaîne alimentaire. Les nutriments permettent d'assurer la croissance du phytoplancton, lui-même consommé par le zooplancton, consommé à son tour par des prédateurs (carnivores de niveau 1 à 4). En favorisant la production primaire, les tourbillons océaniques permettent ainsi l'agrégation de toute la chaîne alimentaire marine via une régulation ascendante (*bottom-up*, Acha *et al.*, 2004; Largier, 1993; Le Fèvre, 1986). Ces tourbillons peuvent aussi être assimilés à des fronts océaniques, caractérisés par des zones de transition à l'interface entre des masses d'eaux aux propriétés contrastées (Belkin *et al.*, 2002; Scales *et al.*, 2014b), et qui présentent une discontinuité physique en terme de température, de salinité ou encore de nutriments (Le Fèvre, 1986; Belkin *et al.*, 2002; Reul *et al.*, 2014; Scales *et al.*, 2014b; Greer *et al.*, 2015). L'exemple de front océanique le plus spectaculaire est situé dans l'Atlantique nord-ouest, où les eaux chaudes et salées du Gulf Stream rencontrent les eaux froides et peu salées du courant du Labrador (Fuglister, 1963).

Bien que ces différentes structures océanographiques soient observées dans la dimension horizontale, et plus particulièrement dans la couche supérieure de la colonne d'eau, elles génèrent également une importante dynamique verticale par le biais d'une multitude de processus physico-chimiques, influençant ainsi les différentes couches de l'écosystème marin.

1.1.2 Variabilité verticale

Circulation thermohaline

En fonction de la latitude et des interactions air-océan (refroidissement, évaporation et précipitation), les masses d'eau des différents bassins océaniques présentent d'importants écarts de densité (Van Haken, 2006). Dans l'Atlantique nord, le courant provenant de la mer du Labrador et de la mer de Norvège est caractérisé par des eaux froides, salées et donc plus denses, qui plongent dans les profondeurs de l'Atlantique (2-3 km de profondeur) en direction de l'océan austral (Broecker, 1997; Dijkstra, 2008; Rahmstorf, 1996) – Figure 1.2. À l'inverse (vers l'océan Indien ou le Pacifique nord), en se réchauffant aux plus basses latitudes (équateur et tropiques), les eaux plus chaudes et moins salées remontent vers la surface. Cette circulation particulière des masses d'eau est appelée circulation thermohaline, et participe au transport de chaleur et de nutriments dans les différents bassins océaniques, depuis les hautes latitudes vers les eaux équatoriales (Wunsch, 2002).

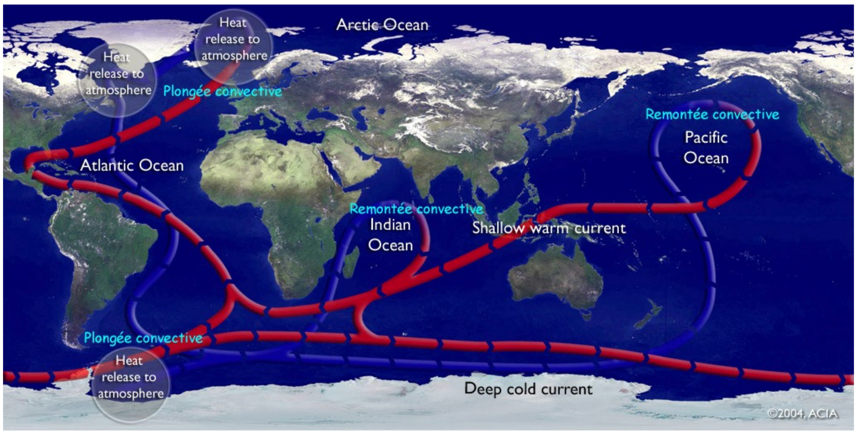


FIGURE 1.2 – Circulation thermohaline (par E. Denous, Université de Lyon). Les courants de surface chauds sont représentés en rouge, tandis que les courants froids situés plus en profondeur sont en bleu.

Spirale d'Ekman et upwelling

Outre la circulation thermohaline, la direction des courants marins est aussi modifiée en profondeur sous l'action du vent et de la force de Coriolis (Ganachaud *et al.*, 2011). Les courants sont ainsi déviés perpendiculairement à la direction du vent, vers la droite dans l'hémisphère nord et vers la gauche dans l'hémisphère sud (Figure 1.3).

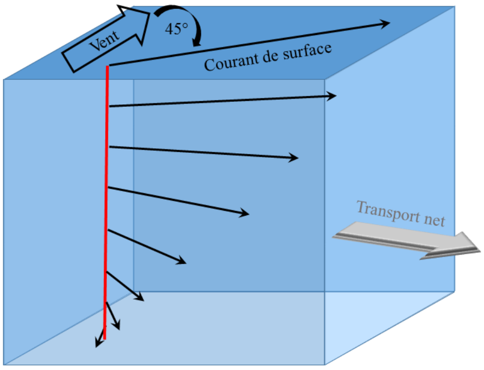


FIGURE 1.3 – Schéma de la spirale d'Ekman.

Ce phénomène est accentué de part et d'autre de l'équateur sous l'influence des alizés, entraînant une divergence de courants de chaque côté de l'équateur. Pour compenser ce phénomène causé par la spirale d'Ekman, des eaux plus froides remontent en surface depuis les profondeurs, c'est ce que l'on appelle un *upwelling*. L'upwelling des Canaries en est un bel exemple, puisqu'il est généré par les vents de surface qui poussent les eaux dans la même direction, parallèle à la côte, faisant ainsi remonter en surface les eaux profondes, riches en nutriments (Raymont, 1980).

Stratification de la colonne d'eau et profils verticaux

À plus fine échelle, la température diminue avec la profondeur en raison de l'absorption massive de chaleur proche de la surface (Williams & Follows, 2011) – Figure 1.4. En hiver, la couche supérieure de la colonne d'eau est brassée sous l'influence des vents, la rendant homogène en termes de température, mais aussi de salinité (et donc de densité). Cette strate homogène, appelée couche de mélange, s'approfondit nettement en hiver, car elle peut atteindre 250 m d'épaisseur au mois de mars dans l'Atlantique nord (Kara *et al.*, 2003). À l'inverse, en été, sous l'effet du transfert de chaleur entre l'atmosphère et la couche supérieure de l'océan, la couche de mélange se réchauffe, devenant moins dense, plus fine et surtout plus stratifiée et donc moins homogène (Williams & Follows, 2011).

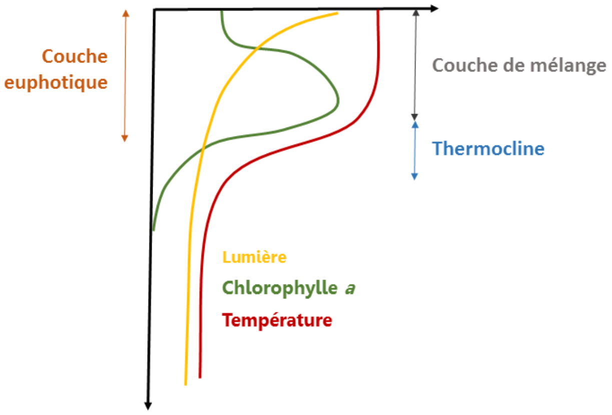


FIGURE 1.4 – Profils verticaux de la température (en rouge), la chlorophylle *a* (en vert) et de l'intensité lumineuse (en jaune) en fonction de la profondeur (schéma inspiré de Ganachaud *et al.* 2011).

Sous cette couche de mélange se trouve la thermocline, une strate caractérisée par un fort gradient thermique (Figure 1.4). En hiver, la turbulence dans la partie supérieure de la colonne d'eau permet la remontée des eaux riches en nutriments plus en surface, entraînant par conséquent la photosynthèse, et donc la production de chlorophylle *a*. En dessous de la couche de mélange, la concentration en chlorophylle *a* diminue drastiquement, tandis que le pic de chlorophylle *a* se situe à la base de la couche de mélange (Figure 1.4).

1.1.3 Effets sur la distribution de la chaîne alimentaire marine

Effets sur la production primaire

La photosynthèse, et par conséquent la production primaire, nécessite à la fois de la lumière et des apports nutritifs, *e.g.* Carbone, Nitrate, Phosphate (Raymont, 1980). Le phytoplancton, composé essentiellement d'organismes unicellulaires (algues et champignons) et qui se déplace passivement dans le milieu pélagique, constitue la base de la chaîne alimentaire marine. En raison de la forte variabilité spatiale de l'océan (*e.g.* courants, masses d'eau et tourbillons) conjuguée à l'effet de la saisonnalité, on observe dans les régions tempérées des blooms phytoplanctoniques au printemps et parfois à l'automne. Aux plus basses latitudes, le pic d'abondance du phytoplancton est plus modéré (Raymont, 1980) – Figure 1.5. La production de chlorophylle *a* par le phytoplancton est ainsi un indicateur de la productivité de l'océan. Dans cet environnement hétérogène, les ressources sont donc très inégalement réparties puisque l'océan est composé à la fois de déserts océaniques, caractérisés par les gyres et donc pauvres en chlorophylle *a* (Parsons *et al.*, 1977), et de zones riches en chlorophylle *a*, et par conséquent riches en proies et prédateurs. Ces oasis de nourriture se situent généralement à proximité des tourbillons, des fronts océaniques ou des côtes, grâce aux apports nutritifs provenant des grands fleuves tels que l'Amazone (Smith & Demaster, 1996) ou le Mississippi (Dortch & Whitledge, 1992) – Figure 1.5.

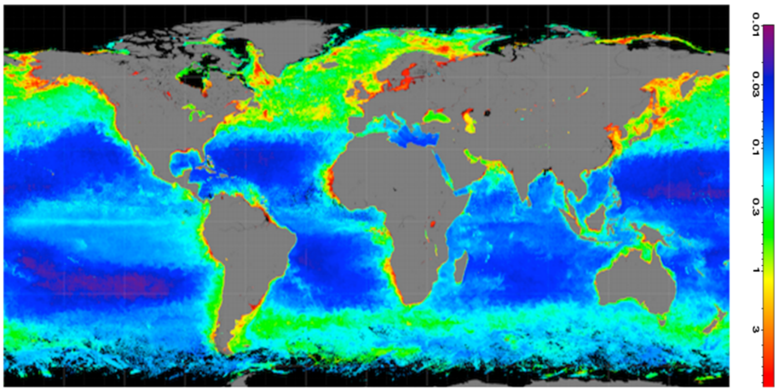


FIGURE 1.5 – Carte de la concentration en chlorophylle *a* dans les océans au mois de juin (en mg.m^{-3}). Carte issue du site oceancolor (satellite MODIS aqua).

Effets sur les déplacements de la mégafaune marine

La répartition inégale des ressources a des conséquences sur toute la chaîne alimentaire marine, générant des associations entre les structures océanographiques et la mégafaune marine telles que les oiseaux marins (Cotté *et al.*, 2007; De Monte *et al.*, 2012; Haney & McGillivary, 1985; Scheffer *et al.*, 2012; Thorne & Read, 2013; Van Franeker *et al.*, 2002; Whitehead *et al.*, 2016), les pinnipèdes (Bailleul *et al.*, 2010; Bradshaw *et al.*, 2004; Dragon *et al.*, 2010; Nordstrom *et al.*, 2013), les cétacés (Doniol Valcroze *et al.*, 2007; Druon *et al.*, 2012; Etnoyer *et al.*, 2006; Moore *et al.*, 2002; Murase *et al.*, 2014) ou encore les tortues marines (Eckert *et al.*, 2006; Fossette *et al.*, 2010a; Polovina *et al.*, 2004; Polovina & Howell, 2005; Witherington, 2002).

1.2 Lien entre environnement marin et déplacements de la mégafaune

La mégafaune marine regroupe l'ensemble des animaux marins de grande taille (Hays *et al.*, 2016), à savoir les oiseaux marins, les mammifères marins (cétacés, pinnipèdes, etc.), les grands poissons pélagiques (requins, thonidés, etc.) ou encore les reptiles (iguanes marins et tortues marines). En raison des distances considérables qu'ils peuvent parcourir en plein océan, l'étude de leurs déplacements en mer s'inscrit dans le domaine de l'écologie du mouvement. L'écologie du mouvement est un domaine de recherche visant à la compréhension des comportements de dispersion, d'alimentation et de migration (Hays *et al.*, 2016).

1.2.1 Déplacements de la mégafaune marine

Le déplacement peut avoir de multiples conséquences sur la *fitness*, la génétique, ou encore sur la dynamique de la population (Dunning *et al.*, 1995; Hanski, 1999; Hanski & Thomas, 1994). La notion de *mouvement* est généralement appliquée à l'échelle individuelle, tandis que le terme *dispersion* peut aussi l'être à l'échelle populationnelle (Cassini, 2013). La *migration* quant à elle, s'applique essentiellement aux déplacements collectifs réalisés à l'échelle de la population.

Cas particulier de la migration

La migration animale correspond au déplacement d'une population d'un endroit à un autre, et d'un retour au point de départ (Schueller & Schueller, 2009). Les distances parcourues par ces organismes migrateurs entre leurs différents habitats peuvent être considérables. Parmi les oiseaux marins migrateurs les plus impressionnants, la Sterne arctique (*Sterna paradisaea*) peut parcourir annuellement jusqu'à 80 000 km entre son site de reproduction en Arctique et ses zones d'alimentation en Antarctique (Egevang *et al.*, 2010; Storr & Storr, 1958) – Figure 1.6.

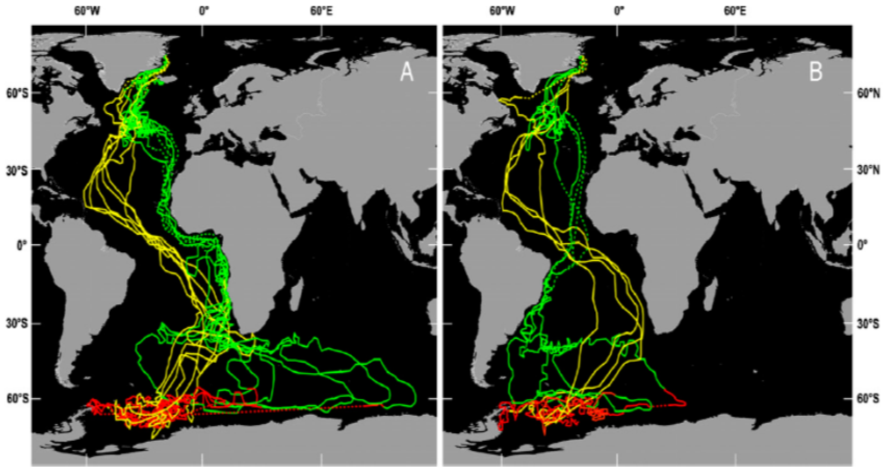


FIGURE 1.6 – Routes migratoires de 11 Sternes arctiques suivies par satellite depuis le Groenland (n = 10) et l'Islande (n = 1, carte issue de Egevang *et al.* 2010). En vert : la migration postnuptiale (août-novembre), en rouge : l'hivernage (décembre-mars), et en jaune : la migration prénuptiale (avril-mai). Deux stratégies ont été adoptées lors de la migration postnuptiale (en vert) dans l'Atlantique sud : le long de la côte ouest de l'Afrique (A) et le long de la côte brésilienne (B).

Chez les mammifères marins, et plus particulièrement chez les cétacés, les baleines à bosse réalisent également d'importantes migrations entre leurs zones d'alimentation situées dans les eaux productives et froides des pôles, et leurs zones de reproduction et de mise bas situées dans les eaux chaudes des tropiques (*e.g.* Fossette *et al.* 2014a; Garrigue *et al.* 2010; Horton *et al.* 2011; Rasmussen *et al.* 2007; Stevick *et al.* 2011). Il existe d'autres groupes de grands migrateurs tels que les pinnipèdes (*e.g.* Hindell *et al.* 2016; Robinson *et al.* 2012), les grands poissons pélagiques (les requins : *e.g.* Skomal *et al.* 2009; Weng *et al.* 2007 ; les thonidés : *e.g.* Block *et al.* 2005, 2001; Wilson *et al.* 2004 ; et les poissons lune : *e.g.* Potter *et al.* 2011), ou encore les tortues marines (*e.g.* Bailey *et al.* 2012b; Fossette *et al.* 2010a; Polovina *et al.* 2000).

Facteurs influençant l'écologie des migrateurs

Le processus migratoire est conditionné par un ensemble de facteurs écologiques et biogéographiques (Alerstam *et al.*, 2003). Ils peuvent être regroupés en deux catégories : (1) les facteurs biotiques et les (2) facteurs abiotiques. Les facteurs (1) biotiques sont principalement la *prédation*, poussant une population à quitter un territoire pour échapper au prédateur, et la *compétition* pour l'accès à la ressource, qui peut se manifester entre des individus provenant d'une même population ou bien entre des individus de populations différentes. Le (2) facteur abiotique le plus important est la *saisonnalité*, qui conditionne la présence ou l'absence de nourriture, la migration étant dans la majorité des cas un comportement adaptatif pour exploiter le pic d'abondance des ressources (Dingle & Drake, 2007). Tout comme les caractéristiques de l'habitat, la saisonnalité permet aussi de réguler la disponibilité de la ressource.

Reproducteur sur capital vs. reproducteur sur revenu

Globalement, un animal migre pour trois raisons principales : la recherche de nourriture, d'un abri ou d'un partenaire (Dingle & Drake, 2007). Un habitat qui présente d'excellentes conditions pour la survie et donc l'activité d'alimentation n'est pas nécessairement favorable à la reproduction, et inversement. Les reproducteurs sur capital cessent de s'alimenter sur leur site de reproduction, utilisant ainsi les réserves acquises durant la période qui précède la migration prénuptiale. Cette stratégie est observée chez la plupart des espèces de tortues marines (Drent & Daan, 1980; Goldberg *et al.*, 2013; Miller, 1997; Rivalan *et al.*, 2005) et l'anguille européenne (van Ginneken & Maes, 2005; Van Ginneken & Van den Thillart, 2000). Par contre, les reproducteurs sur revenu quant à eux s'alimentent au cours de la période de reproduction, utilisant ainsi le même habitat pour la prospection alimentaire et la reproduction (Drent & Daan, 1980; Milner-Gulland *et al.*, 2011). Toutefois, certaines espèces, comme le puffin des Anglais, réalisent des haltes migratoires pour s'alimenter au cours de la migration (Guilford *et al.*, 2009).

1.2.2 Méthodes d'échantillonnage

L'observation des déplacements des animaux marins nécessite plusieurs techniques d'échantillonnage complémentaires, allant de l'observation directe, à l'aide de la méthode de Capture-Marquage-Recapture (CMR), au suivi satellitaire ou encore au biologging.

Capture-Marquage-Recapture (CMR)

La première étape pour étudier les déplacements des animaux dans leur milieu naturel est de s'assurer qu'ils peuvent être identifiés de manière unique après leur marquage (McCrea & Morgan, 2014). Certains animaux peuvent être identifiés à l'aide de leurs caractéristiques physiques (*e.g.* cicatrices, tâches ou forme de l'aileron dorsal). C'est le cas par exemple de la photo-identification des cétacés, qui implique la photographie de leur nageoire caudale, propre à chaque individu (Rock *et al.*, 2006). Les animaux peuvent aussi être marqués d'une bague portant un numéro unique, ce qui permet de connaître la provenance des individus lors de chaque recapture. Cette méthode n'implique pas nécessairement une capture/recapture physique de l'individu dans la mesure où la marque ou le numéro peuvent être observés visuellement ou identifiés électroniquement. Elle a été largement utilisée depuis les années 1950 sur une variété d'espèces, notamment sur les manchots pour étudier leurs déplacements, mais aussi leurs traits d'histoire de vie (Sladen & Penney, 1960; Weimerskirch *et al.*, 1992). L'utilisation de transpondeurs se répand de plus en plus, car elle consiste à insérer un transpondeur RFID (*radio frequency identification*) sous la peau de l'animal, ce qui permet une identification automatique tout en évitant la gêne occasionnée par les bagues (Saraux *et al.*, 2011). Leur extrême miniaturisation est rendue possible par l'absence de batterie, l'identification étant assurée lorsque l'animal auquel le transpondeur a été implanté passe à proximité d'un champ électromagnétique produit par une antenne. Cette identification sur des lieux de passage approprié permet de savoir si un individu est encore vivant, et s'il s'agit de lieu du reproduction, de savoir quand il se reproduit et s'il le fait avec succès. Associée à cette identification RFID, une pesée électronique permet d'évaluer les réserves corporelles de l'animal sans le perturber. Les deux principales contraintes de la RFID sont la faible distance de lecture et l'absence de signe visible permettant de localiser l'animal transpondé, d'où de nouvelles méthodes comme l'utilisation de ROVs (*remotely operated vehicles*) permettant d'approcher les animaux sans les perturber (Le Maho *et al.*, 2014).

La CMR permet ainsi de constituer une solide base de données afin de reconstituer les différents trajets migratoires des animaux. Cette technique est largement utilisée chez les tortues marines, en particulier chez les femelles adultes gravides, qui sont le plus souvent observées lors de la ponte à terre. Ainsi, les données issues des bagues ou des transpondeurs ont permis d'établir des connexions entre différents sites de ponte et d'alimentation des tortues marines, comme c'est le cas pour certaines tortues vertes adultes qui ont été marquées en Guyane française, et de nouveau observées au large de l'état du Ceará au Brésil (Pritchard, 1976). D'autres tortues vertes, cette fois immatures, ont été marquées aux Bermudes, et de nouveau observées dans différentes régions des Caraïbes (*e.g.* Floride, République dominicaine, Panama, Cuba ou encore Nicaragua ; Meylan *et al.* 2011) - Figure 1.7.

FIGURE 1.7 – Carte illustrant les 88 recaptures de tortues vertes immatures, initialement marquées aux Bermudes (carte issue de Meylan *et al.* 2011).

Malgré le grand intérêt des techniques de bagage, elles présentent toutefois certaines limites. Depuis les années 1970, plusieurs études ont mis en évidence un effet délétère des bagues aux ailerons des manchots. Elles peuvent blesser les tissus de l'animal, notamment lorsqu'ils s'épaississent au cours de la mue, et elles altèrent son hydrodynamique et donc ses performances alimentaires (Jackson & Wilson, 2002; Wilson, 2011; Le Maho *et al.*, 2011; Saraux *et al.*, 2011). Chez les tortues marines, une étude a également révélé l'effet néfaste du transpondage chez les femelles caouannes qui semblent retourner prématurément à la mer avant d'avoir totalement recouvert leurs œufs après la ponte (Broderick & Godley, 1999). De plus, les techniques de CMR ne permettent pas de suivre de manière continue les déplacements des animaux, ce qui est rendu possible grâce à l'utilisation de la télémétrie.

Suivi télémétrique

L'émergence de la télémétrie remonte aux années 1950 (Gillespie, 2001). Elle consiste à transmettre à distance des données à partir d'émetteurs fixés directement sur les animaux (Hays *et al.*, 2016). Les méthodes traditionnelles pour suivre les déplacements des animaux terrestres impliquaient l'utilisation de radars ou de bandes de très hautes fréquences

(VHF) via la radiotélémétrie (Gillespie, 2001). À la différence de la radiotélémétrie qui nécessite un observateur au sol pour localiser l'animal par triangulation, le suivi satellitaire permet de suivre les déplacements d'animaux sur de très longues distances, aussi bien terrestres que marins, tout en transmettant les informations en temps quasi réel. Ainsi, chez les animaux marins, les balises satellites peuvent collecter un ensemble de paramètres relatifs au comportement (*e.g.* trajectoire et comportement de plongée), à la physiologie (*e.g.* température corporelle) et aux milieux dans lesquels les individus se déplacent (*e.g.* température, salinité, luminosité et fluorescence). Ces 20 dernières années, les grandes avancées technologiques dans le domaine de la télémétrie ont permis de miniaturiser les appareils et d'augmenter leur autonomie, fournissant ainsi des informations capitales sur les schémas migratoires d'une multitude d'espèces marines. À titre d'exemple, dans l'océan Pacifique, le programme Tagging of Pacific Predators (TOPP) a permis d'identifier les routes migratoires de 23 espèces marines différentes, à l'aide de 4306 balises déployées (Block *et al.*, 2011) – Figure 1.8. Outre l'amélioration de la connaissance sur l'écologie en mer des prédateurs marins, la télémétrie fournit également une base scientifique solide pour identifier les zones critiques à prioriser et ainsi contribuer à la conservation de ces espèces, dont les populations de la plupart d'entre elles sont en déclin (Hays *et al.*, 2016).

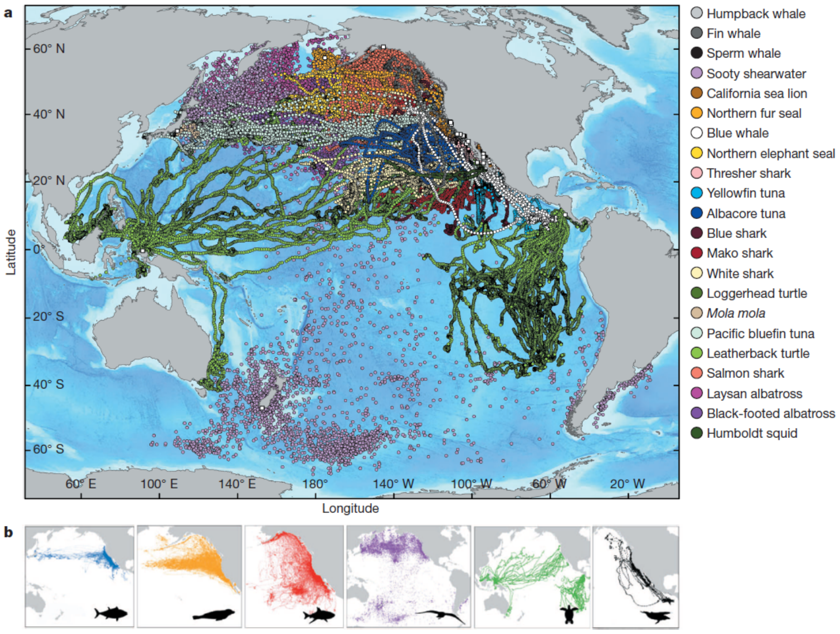


FIGURE 1.8 – (**a**) Carte des positions moyennes journalières des différents groupes de prédateurs équipés de balises satellitaires dans le Pacifique (issu de Block *et al.* 2011). (**b**) Cartes des positions moyennes journalières des principaux groupes, de gauche à droite : thonidés, pinnipèdes, requins, oiseaux marins, tortues marines et cétacés.

Échantillonnage de l'environnement marin

L'échantillonnage direct de la colonne d'eau est réalisé grâce à l'utilisation de sondes CTD (*Conductivity Temperature Depth*), qui permettent de mesurer la conductivité et la température de l'eau, ainsi que la profondeur (Pennington & Chavez, 2000). À l'inverse des balises satellitaires ou des *biologgers*, ce type d'échantillonnage nécessite un bateau qui permet de réaliser des prélèvements à des stations fixes (position et profondeur), limitant ainsi la couverture spatiale et temporelle.

Un autre moyen d'accéder à de telles informations est l'utilisation de balises satellites déployées sur la mégafaune marine, ce qui permet de collecter des informations sur l'environnement physique (*e.g.* température et salinité de l'eau) et biologique (*e.g.* fluorescence comme indicateur de la concentration en chlorophylle *a*) traversé par ces animaux. L'utilisation de la télémétrie ou du biologging pour échantillonner l'écosystème marin s'avère extrêmement utile lorsque l'on s'intéresse à des zones difficiles d'accès ou sous-échantillonnées, comme c'est le cas par exemple pour les régions polaires (*e.g.* Charrassin *et al.* 2008; Lydersen *et al.* 2002; Roquet *et al.* 2013).

Afin de permettre l'échantillonnage de profils de température/salinité à différentes profondeurs et de couvrir une plus large zone sans avoir recours à des relevés de sondes en bateau, le lancement du programme ARGO en 2000 a permis de déployer annuellement près de 800 flotteurs (Gould *et al.*, 2004; Roemmich *et al.*, 2001, 2009, 2004). À ce jour, ce programme compte près de 3800 flotteurs dans les différents océans du globe. Ils mesurent en continu la température et la salinité de l'eau, de la surface jusqu'à 2000 m de profondeur. En complément des flotteurs ARGO, l'utilisation de la télédétection spatiale via les mesures effectuées par les satellites (*e.g.* MODIS, SeaWIFS) permet d'observer et de surveiller en continu l'océan, sur des échelles allant du local au global (Martin, 2014). La télédétection spatiale fournit ainsi des données complémentaires aux sondes CTD et aux flotteurs ARGO, en calculant notamment la hauteur d'eau (Sea Surface Height : SSH), la température de surface de l'eau (Sea Surface Temperature : SST), la vitesse du vent, des courants, etc. Au fur et à mesure des avancées scientifiques et technologiques, l'association des données satellitaires aux données *in situ* a permis l'émergence de puissants modèles océaniques tels que Copernicus-MyOcean (Adragna & Bahurel, 2009) ou encore HYCOM (*HYbrid Coordinate Ocean Model*, Chassignet *et al.* 2007). Ces bases de données environnementales fournissent de précieux outils pour étudier les déplacements de la mégafaune marine en lien avec son habitat, permettant ainsi de mieux comprendre comment ces espèces utilisent et sélectionnent leur environnement.

1.2.3 Utilisation de l'habitat à partir de données télémétriques

L'étude de l'utilisation de l'habitat consiste à faire le lien entre les déplacements des animaux et les caractéristiques de leur environnement (leur habitat). Au sein de son habitat, un animal peut en effet adopter une série de comportements différents : repos, reproduction, alimentation, etc. À partir de données télémétriques, l'objectif premier est donc (1) d'identifier les zones utilisées de manière préférentielle par l'individu, puis (2) d'établir le lien qui existe entre ces zones et les caractéristiques de son habitat (*e.g.* facteurs biologiques, physiques). Selon le type de données dont on dispose et la question posée, il existe plusieurs outils disponibles pour identifier ces zones préférentielles : estimation par noyau, temps de résidence, indice de chasse, etc.

Estimation du domaine vital

Déterminer l'utilisation de l'espace par un animal est crucial pour assurer sa conservation (Hoenner *et al.*, 2012). C'est pourquoi, lorsque l'objectif de l'étude est de quantifier la surface utilisée par un individu dans une perspective de conservation (*e.g.* délimitation d'une aire marine protégée), différentes méthodes peuvent être employées, comme l'estimation par noyau ou encore le temps passé par cellule. Ces méthodes sont généralement employées pour estimer la fidélité à un site lorsque les individus présentent un comportement de résidence, *e.g.* les tortues marines sur leur site de reproduction/d'inter-ponte ou d'alimentation (*e.g.* Hart *et al.* 2013, 2012; Maxwell *et al.* 2011; Schofield *et al.* 2010), ou encore les oiseaux marins sur leurs aires d'alimentation (Thiers *et al.*, 2014b,a) – Figure 1.9.

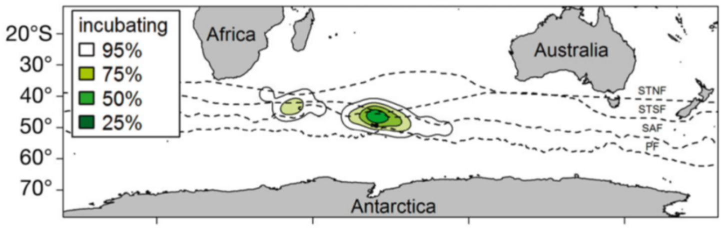


FIGURE 1.9 – Contours issus des densités de Kernel réalisées à partir des positions de Pétrels géants du nord suivis par GPS durant la période d'incubation depuis Kerguelen (issu de Thiers *et al.* 2014b).

Toujours à partir des données de télémétrie, le calcul du temps passé par cellule constitue une autre approche pour identifier les zones clés de concentration d'individus (Dodge *et al.*, 2014; James *et al.*, 2005; Stokes *et al.*, 2015). Un bel exemple de cette approche est l'étude de Stokes *et al.* (2015) réalisée à partir des trajectoires de 29 tortues vertes adultes, suivies par satellite depuis leurs sites de reproduction dans le Bassin méditerranéen jusqu'à leurs zones d'alimentation respectives, dispersées le long de l'Afrique du

Nord (Figure 1.10). Étant donné le fort taux de captures accidentelles de tortues marines dans les filets de pêche en Méditerranée, cette étude a permis de mettre en évidence les couloirs migratoires ainsi que les zones d'alimentation utilisées par cette espèce d'une année sur l'autre, pour ainsi faciliter la mise en place de mesures de gestion adaptées afin d'assurer la conservation de cette espèce.

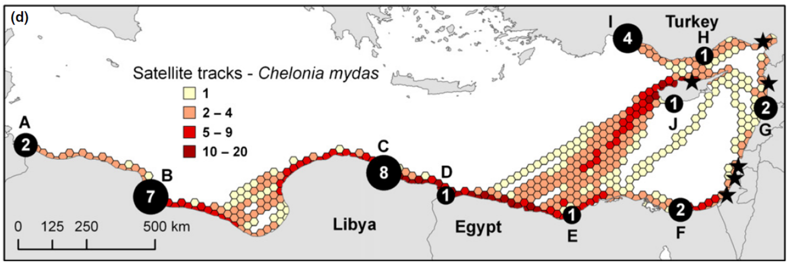


FIGURE 1.10 – Carte du temps passé par cellule (en jours) issue des trajectoires de 29 tortues vertes femelles suivies par satellite (issu de Stokes *et al.* 2015). Les nombres correspondent au nombre d'individus suivis consécutivement jusqu'à chaque zone d'alimentation.

Détection de zones de recherche restreinte

Lorsque l'habitat est utilisé à des fins de prospection alimentaire, généralement le comportement des animaux change nettement. Ceci est indiqué tout d'abord par une modification des trajectoires, mais aussi par une diminution de la vitesse de nage associée à une augmentation de la sinuosité (Kareiva & Odell, 1987; Robinson *et al.*, 2007). La détection de ces zones de recherche restreinte (*Area-Restricted Search* : ARS) a permis d'identifier un comportement de prospection alimentaire chez de nombreuses espèces de mégafaune marine telles que les pinnipèdes (*e.g.* Bailleul *et al.* 2008; Dragon *et al.* 2012; Heerah *et al.* 2016; Tremblay *et al.* 2009), les cétacés (*e.g.* Bailey *et al.* 2009; Lemieux Lefebvre *et al.* 2012), les oiseaux marins (*e.g.* Lescrol & Bost 2005; Pinaud 2008; Pinaud & Weimerskirch 2007; Scheffer *et al.* 2010) et les tortues marines (*e.g.* Bailey *et al.* 2012b; Fossette *et al.* 2010a; Jonsen *et al.* 2007a, 2006; McCarthy *et al.* 2010; Shaver *et al.* 2013; Shillinger *et al.* 2008) – Figure 1.11. Étant donné l'importance de la structure verticale de la colonne d'eau dans certaines zones d'agrégation des proies (Fuiman *et al.*, 2002; Mitani *et al.*, 2003; Watanabe *et al.*, 2003), il est également capital d'inclure la dimension verticale dans la détection des ARS. En effet, plusieurs indicateurs de l'effort de chasse au sein des plongées ont été développés ces dernières années (*e.g.* Bailleul *et al.* 2008; Heerah *et al.* 2015, 2016, 2014).

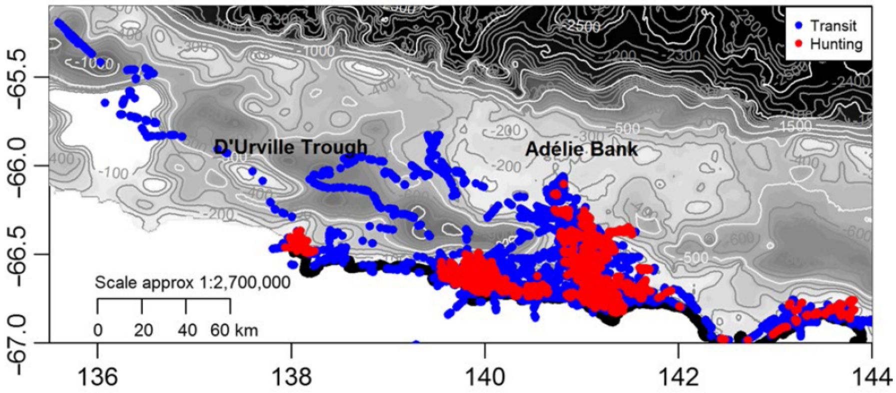


FIGURE 1.11 – Positions des plongées réalisées par 12 phoques de Weddel suivis par satellite depuis Dumont D'Urville (Heerah et al 2016). À partir de la méthode du temps de chasse (issu de Heerah *et al.* 2014), un mode comportemental a pu être assigné à chaque plongée : transit en bleu et prospection alimentaire en rouge (hunting).

Lien avec l'habitat

Après avoir identifié les zones préférentiellement utilisées, il est donc possible de relier le comportement des animaux aux caractéristiques de leur habitat. Les variables de l'environnement marin le plus communément utilisées dans l'étude de l'habitat peuvent être regroupées en trois grandes catégories :

1. Les variables physiographiques :
    - La *bathymétrie* des océans. Elle peut influer sur la distribution des proies selon que l'on s'intéresse à un prédateur pélagique ou benthique. Chez l'éléphant de mer austral par exemple, il a été mis en évidence une forte affinité pour les faibles profondeurs chez les femelles adultes (Labrousse *et al.*, 2015).
    - La *pente*. Généralement déduite de la bathymétrie, elle renseigne sur le domaine étudié, *e.g.* le plateau continental ou la pente océanique. Cette dernière sépare le plateau continental de l'océan ouvert. Dans le Pacifique sud par exemple, des associations entre de fortes concentrations de globicéphales et de fortes pentes ont été observées (Mannocci *et al.*, 2014).
2. Les variables océanographiques :
    - La *température de l'eau*. En surface (SST) ou encore en profondeur, elle permet entre autres d'identifier la profondeur de la thermocline, zone de fort gradient thermique, connue pour agréger toute une faune marine (*e.g.* Bailey *et al.* 2012b; Charrassin & Bost 2001; Hakoyama *et al.* 1994). Le lien entre déplacements et température de surface peut à la fois renseigner sur les tolérances thermiques d'une espèce, ou bien sur celles de ses proies.

- La *hauteur d'eau* et les *courants marins* (direction et vitesse). Ils permettent d'identifier les zones tourbillonnaires, auxquelles sont associées de nombreuses espèces marines (*e.g.* Moore *et al.* 2002; Polovina *et al.* 2006; Whitehead *et al.* 2016)- Figure 1.12.
- La *salinité*. Elle constitue un indicateur des apports nutritifs en provenance des fleuves, qui peuvent renseigner sur des zones productives enrichies en production primaire (Mannocci *et al.*, 2015).

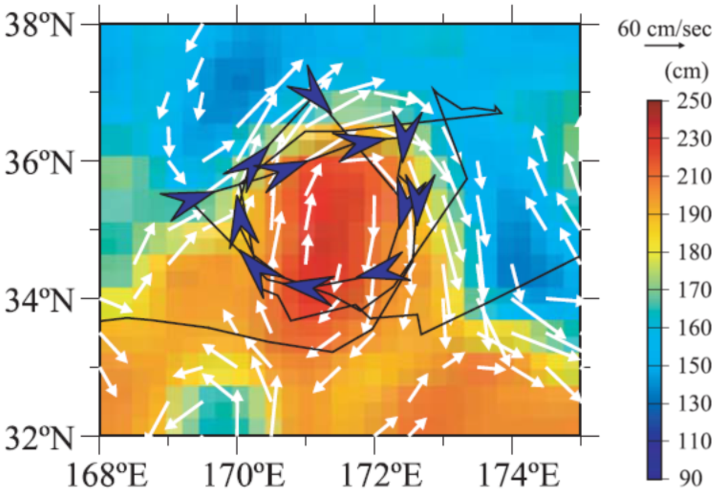


FIGURE 1.12 – Association entre les courants (flèches blanches) et la trajectoire d'une tortue caouanne suivie par satellite (issu de Polovina *et al.* 2006). Le code couleur correspond à la hauteur d'eau permettant d'identifier la présence de tourbillons anticycloniques.

3. Les variables biologiques :

- La *profondeur de la couche euphotique*. Elle correspond à la strate supérieure de la colonne où il y a suffisamment de lumière pour permettre la photosynthèse. Cette couche euphotique renseigne sur la variabilité verticale de l'accès à la ressource. Une récente étude de Lambert *et al.* (2014) a montré que les delphinidae de l'océan indien utilisent de manière préférentielle des zones associées à des profondeurs euphotiques faibles.
- La *concentration en chlorophylle a*, ou la productivité primaire. Elles sont communément utilisées comme un indicateur de la productivité marine. Par exemple, il a été montré que les tortues luths de l'Atlantique nord se distribuent préférentiellement dans les eaux productives au cours de la migration, là où la concentration en chlorophylle *a* est plus élevée (Dodge *et al.*, 2014), et probablement plus riche en proies.

1.3 Des migratrices particulières : les tortues marines

Il existe sept espèces de tortues marines dans le monde, dont six appartiennent à la famille des Cheloniidae, aussi appelées tortues à écailles (Dutton *et al.*, 1999; Lutz & Musick, 1996), *i.e.* la tortue verte (*Chelonia mydas*), la tortue caouanne (*Caretta caretta*), la tortue imbriquée (*Eretmochelys imbricata*), la tortue olivâtre (*Lepidochelys olivacea*), la tortue de kemp (*Lepidochelys kempii*) et la tortue à dos plat (*Natator depressus*). La dernière espèce, la tortue luth (*Dermochelys coriacea*), ne dispose pas d'écaille et appartient à la famille des Dermochelyidae, qui a divergé de la famille de Cheloniidae il y a environ 100-150 millions d'années (Dutton *et al.*, 1999). Majoritairement distribuées dans la ceinture intertropicale (Lutz & Musick, 1996), ces sept espèces de tortues marines présentent une grande diversité dans leurs schémas d'histoire de vie, utilisant différents habitats selon leur stade de développement.

1.3.1 Un cycle de vie complexe

Le cycle de vie des tortues marines est complexe puisqu'elles utilisent une multitude d'habitats au cours de leurs stades de développement, évidemment terrestres lors de la ponte et l'éclosion, côtiers ou océaniques lors de la reproduction ou la migration.

Les schémas d'histoire de vie

Selon les types d'habitats utilisés, on distingue trois schémas d'histoire de vie principaux (Bolten, 2003) :

- Type 1. Le développement en milieu exclusivement néritique, ce qui signifie que les juvéniles et les adultes passent l'intégralité de leur vie en milieu côtier (Figure 1.13 à gauche). C'est le cas de la tortue à dos plat d'Australie (Walker & Parmenter, 1990). L'augmentation de la ressource en milieu néritique est contrebalancée par l'augmentation de la pression de prédation, ce qui expliquerait pourquoi les émergences (nouveau-nés) de la tortue à dos plat sont plus grandes que celles des autres espèces de la même famille (les Cheloniidae, 6 cm pour 39 g *vs.* 4,1-5 cm pour 15-25 g).

- Type 2. Le développement des juvéniles se déroule en milieu océanique, tandis que les adultes évoluent en milieu néritique (Figure 1.13 au centre). Ce type de schéma de développement concerne la majorité des tortues à écailles, *i.e.* tortue verte, tortue imbriquée, tortue caouanne, tortue de kemp et tortue olivâtre.

- Type 3. Le développement en milieu océanique concerne essentiellement la tortue luth, qui, en dehors de la ponte, passe l'intégralité de sa vie en plein océan, loin des côtes (Figure 1.13 à droite). Bien que la tortue olivâtre semble adopter le schéma de type 2 dans l'Atlantique occidental et l'Australie, cette espèce adopte majoritairement le schéma de type 3 dans le Pacifique (Pitman, 1990).

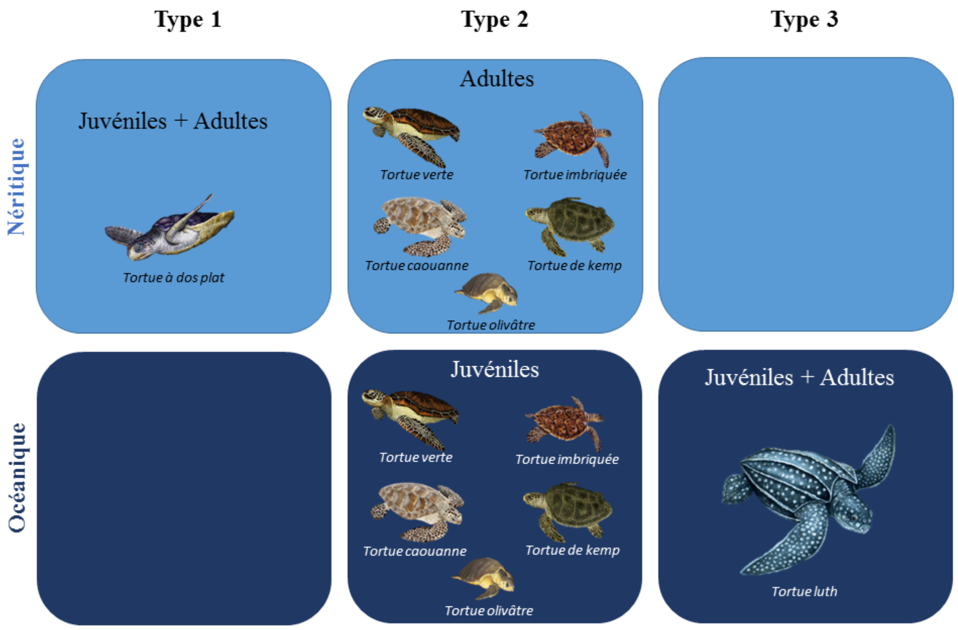


FIGURE 1.13 – Les trois types de schémas de développement des tortues marines en fonction de l'habitat occupé (néritique en bleu clair *vs.* océanique en bleu foncé) et du stade (juvénile *vs.* adulte).

Les stades ontogénétiques

Selon l'espèce et le stade de développement (stade ontogénétique : juvénile, adulte), les tortues marines utilisent différents habitats, que l'on peut regrouper en cinq grandes catégories (Musick & Limpus, 1997) - Figure 1.14 :

1. L'habitat océanique des émergences/juvéniles. Juste après l'éclosion, les jeunes tortues (émergences) rejoignent la mer le plus rapidement possible, puis s'éloignent de la bande côtière, riche en prédateurs (*e.g.* poissons, requins, oiseaux marins) pour rejoindre le domaine pélagique. Elles passent ensuite plusieurs années de leur vie en plein océan, leurs déplacements étant dictés à la fois par les courants marins et de la nage active, et ce, malgré leur petite taille (Mansfield & Putman, 2013) – Figure 1.14. Les déplacements des jeunes tortues évoluant en plein océan ont longtemps été décrits comme une migration passive, uniquement dictée par les courants marins (Bolten, 2003; Carr, 1987; Luschi *et al.*, 2003b; Witherington, 2002; Putman & Naro-Maciel, 2013). Hors, de récentes études réalisées à partir de simulations de modèles océaniques incluant de la nage active, ont démontré que les trajectoires des

jeunes tortues de l'Atlantique nord et du golfe du Mexique sont façonnées par l'action conjuguée des courants marins et d'une nage orientée (Mansfield *et al.*, 2014; Putman & Mansfield, 2015; Putman *et al.*, 2012a,b, 2014; Briscoe *et al.*, 2016).

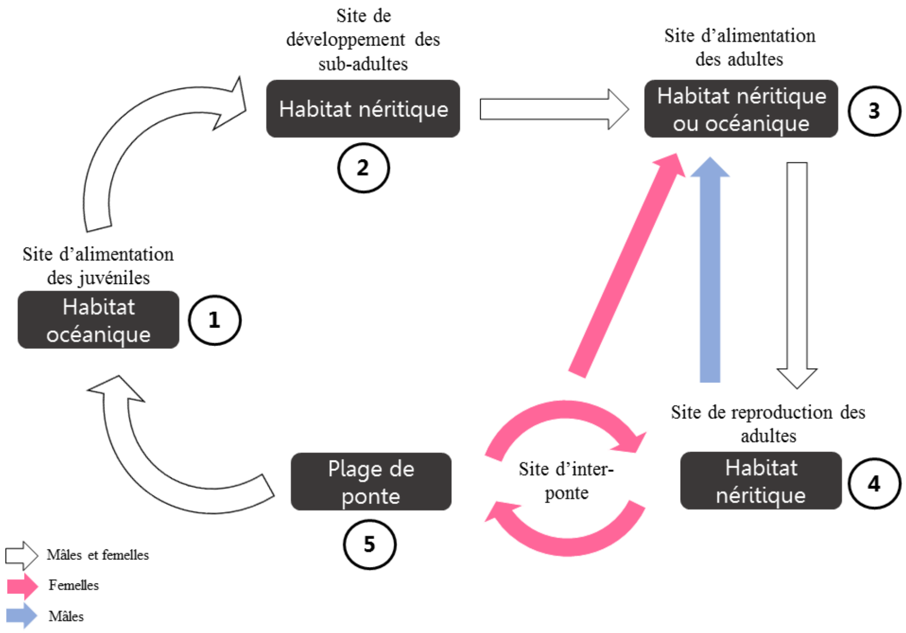


FIGURE 1.14 – Cycle de vie des tortues marines avec les différents stades ontogénétiques, et pour les deux sexes (femelles en rose, mâles en bleu, les deux sexes combinés en blanc).

2. L'habitat néritique de développement des subadultes. Après avoir grandi pendant plusieurs années en plein océan, les juvéniles rejoignent des habitats néritiques dits de développement, où ils poursuivent leur croissance jusqu'à la maturité sexuelle (Musick & Limpus, 1997) - Figure 1.14. Par exemple, chez la tortue caouanne de l'Atlantique nord, la phase dite de recrutement (le moment où les jeunes tortues quittent l'habitat océanique) a lieu lorsque les individus mesurent entre 25 et 30 cm (de longueur curviligne), c'est-à-dire à l'âge de 7 à 10 ans (Musick & Limpus, 1997). Ces habitats fournissent à la fois un refuge vis-à-vis des prédateurs, mais aussi une quantité suffisante de nourriture, comme c'est le cas dans la région Caribéenne-Atlantique (Godley *et al.*, 2003; Hart *et al.*, 2010; Makowski *et al.*, 2005; Meylan *et al.*, 2011).

3. L'habitat d'alimentation des adultes. Une fois la maturité sexuelle atteinte, les tortues subadultes quittent leur habitat de développement, entamant ainsi leur migration vers les zones d'alimentation des adultes (Figure 1.14). Chez certaines populations, l'habitat d'alimentation des adultes est éloigné géographiquement de l'habitat de développement des subadultes, mais ce n'est pas toujours le cas. La plupart des

espèces de tortues marines présentent une grande fidélité à leurs zones d'alimentation. Des tortues vertes et tortues caouannes suivies par satellite en Méditerranée ont emprunté les mêmes routes et se sont rendues sur les mêmes zones d'alimentation d'une année sur l'autre (Broderick *et al.*, 2007). Toutefois, la longue durée de leur migration rend difficile le suivi à terre des mêmes individus d'une saison de ponte à l'autre, puisque certaines espèces comme la tortue verte peuvent passer jusqu'à cinq années consécutives en pleine mer avant de revenir sur leur site de ponte pour y déposer leurs œufs (Hamann *et al.*, 2002).

4. L'habitat de reproduction des adultes. Après avoir passées plusieurs années en migration à s'alimenter, les tortues marines rejoignent leurs zones de reproduction (Miller, 1997), généralement situées à proximité de leur plage natale (Limpus & Limpus, 1993; Owens & Morris, 1985) - Figure 1.14.

5. L'habitat d'inter-ponte des femelles adultes. Les femelles ont la particularité de revenir pondre sur leur plage de naissance. Après avoir été fécondées, les femelles entament une série d'allers-retours entre leur site de reproduction en mer et leur plage de ponte, et ce, pour y déposer leurs œufs plusieurs fois par saison (Miller, 1997). Cette période correspond à la saison d'inter-ponte (Figure 1.14), et peut durer plusieurs mois (Schofield *et al.*, 2013b) au cours desquels les femelles vont venir pondre en moyenne une centaine d'œufs. Ainsi, en une saison de ponte, les tortues luths viennent pondre en moyenne entre quatre à sept fois (Reina *et al.*, 2002).

1.3.2 Les sites de ponte de l'Atlantique tropical

La côte nord-est de l'Amérique latine

Les eaux de l'Atlantique tropical hébergent cinq des sept espèces de tortues marines présentent dans le monde, *i.e.* tortue caouanne, imbriquée, verte, luth et olivâtre (Mast *et al.*, 2016) – Figure 1.15. En effet, la côte nord-est de l'Amérique latine ainsi que les Caraïbes abritent de nombreux sites de ponte pour ces cinq espèces. Sur les 38 sous-populations (aussi appelé *Regional Management Units* : RMU) de tortues marines identifiées dans les différents océans du globe, l'Amérique latine compte 12 RMUs. Ainsi, la région des Guyanes, qui s'étend du Guyana au nord du Brésil (délimité par le fleuve Amazone), est connue pour abriter un grand nombre de sites de ponte de tortues vertes, de tortues olivâtres et de tortues luths.

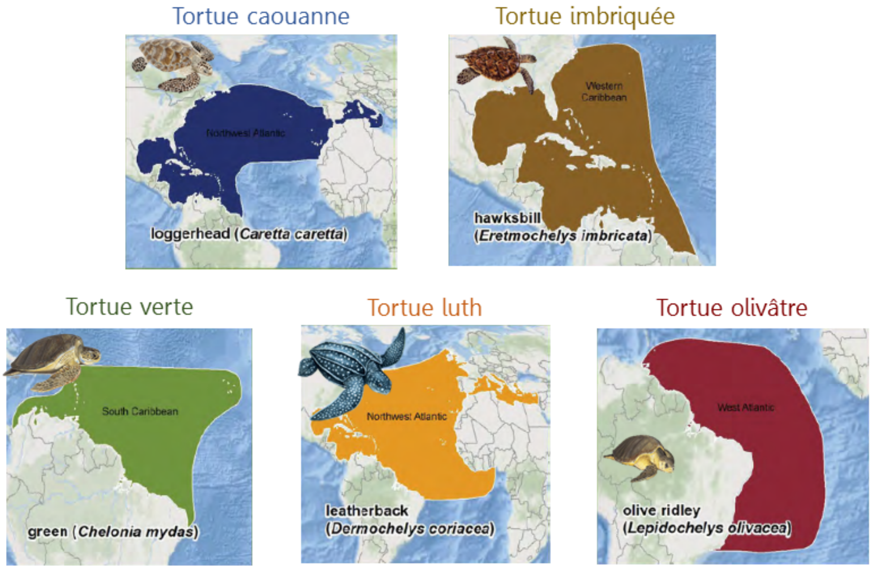


FIGURE 1.15 – Unités régionales de gestion (RMUs) identifiées le long de la côte nord-est de l'Amérique latine pour chaque espèce (issu de Mast *et al.* 2016).

La côte de Guyane française

Sur les 378 km de côte qu'offre la Guyane française, deux sites de ponte principaux de quelques kilomètres de long font l'objet d'un suivi régulier depuis maintenant 47 ans. Bien que cinq des sept espèces de tortues marines présentent dans le monde nidifient sur le littoral guyanais, seulement trois d'entre elles (tortue olivâtre, tortue verte et tortue luth) sont observées chaque année en grand nombre sur les plages de Guyane française. La tortue imbriquée et la tortue caouanne ne sont observées qu'occasionnellement (Bioinsight DIREN Guyane, 2003).

1. Le site d'Awala-Yalimapo. Situé à l'ouest de la Guyane française, à la frontière Surinamaise, ce site de ponte a été découvert dans les années 1960 (Mast *et al.*, 2016). Depuis les années 1970, un suivi annuel des deux populations de tortues vertes et de tortues luths a été mis en place sur ce site (Girondot & Fretey, 1996; Rivalan *et al.*, 2005) - Figure 1.16. Classée en danger d'extinction sur la liste rouge de l'Union Internationale pour la Conservation de la Nature (UICN), la tortue verte *Chelonia mydas* est herbivore à l'âge adulte, se nourrissant principalement d'herbiers et de phanérogames marines (Bjorndal 1997, Tableau 1.1). Il s'agit de la plus grande des tortues à écailles. En Guyane française, une femelle adulte mesure en moyenne 113 cm et pèse environ 180 kg (Chevallier, communication personnelle). En Guyane française, la ponte a lieu tous les trois ans en moyenne, entre le mois de février et le mois de juin. Au cours de la saison dite d'inter-ponte (période comprenant les différentes pontes successives avant le départ en migration), la tortue verte revient

environ tous les 13 jours pour pondre en moyenne 120 œufs (Chevallier, communication personnelle). En 2015, un total de 2228 pontes a été recensé pour cette espèce à Yalimapo (Mast *et al.*, 2016), ce qui en fait l'un des plus grands sites de ponte de la côte nord-est de l'Amérique latine pour cette espèce, puisqu'il s'étend de part et d'autre du fleuve Maroni, jusqu'aux plages du Suriname (Schulz, 1975). Malgré son effectif important sur les plages guyanaises et ses grandes migrations, la tortue verte n'a pas encore fait l'objet d'un suivi satellitaire au départ de la Guyane française.

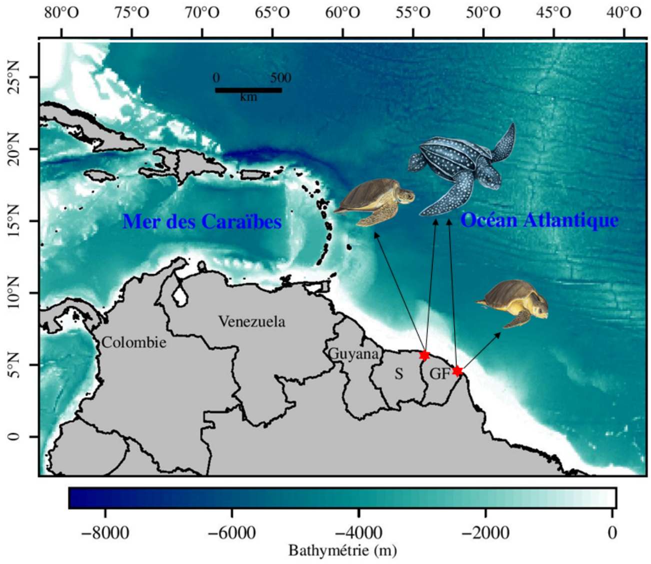
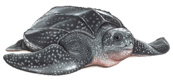


FIGURE 1.16 – Zone d'étude correspondant aux deux sites de ponte de ponte de la Guyane française (étoiles rouges) et aux trois espèces de tortues marines faisant l'objet d'investigations (de gauche à droite : tortue verte, tortue luth et tortue olivâtre). GF correspond à Guyane française et S à Suriname.

Tandis que la population de tortues vertes de Yalimapo semble croître au fil des années (531 pontes observées en 2005 *vs.* 2228 en 2015), la population de tortues luths est en déclin depuis les années 1990 (7260 pontes en 2005 *vs.* 483 en 2015, ONCFS) – Figure 1.16. Cette espèce est classée vulnérable sur la liste rouge de l'UICN, et c'est la plus imposante des tortues marines, mesurant en moyenne 155 cm de long, et pouvant peser jusqu'à 400 kg pour une femelle adulte (Girondot & Fretey 1996; Fossette *et al.* 2010a, Tableau 1.1). C'est également la seule à se nourrir exclusivement de macrozooplancton gélatineux (*e.g.* mésuses scyphozoaires, pyrosomes, siphonophores) durant tout son cycle de vie (Davenport, 1998), et à se rendre dans les eaux froides des hautes latitudes (> 30 °N et < 30 °S). Sur la plage de Yalimapo, la saison de ponte de la tortue luth s'étend de fin février à début août, période au cours de laquelle elle revient pondre environ tous les 10 jours pour y déposer entre 80 et 100 œufs (Girondot & Fretey, 1996). Au début des années 2000, l'émergence de la télémétrie a permis de suivre les déplacements de dizaines de tortues luths femelles adultes au départ d'Awala-Yalimapo, à la fois pendant l'inter-ponte (Fossette *et al.*, 2008c, 2007; Georges *et al.*, 2007), mais aussi durant sa migration océanique (Ferraroli *et al.*, 2004; Fossette *et al.*, 2010b,a; Hays *et al.*, 2004a).

Tableau 1.1 – Caractéristiques des trois espèces de tortues marines présentent sur les deux sites de ponte de Guyane française.

Espèce	 **Tortue olivâtre** *Lepidochelys olivacea*	 **Tortue verte** *Chelonia mydas*	 **Tortue luth** *Dermochelys coriacea*
Taille moyenne (cm)	70	113	160
Poids moyen (kg)	40	180	400
Statut UICN	Vulnérable	En danger	Vulnérable
Régime alimentaire	Carnivore	Herbivore	Zooplanctivore
Site de ponte en Guyane française	Awala-Yalimapo	Rémire-Montjoly	Awala-Yalimapo & Rémire-Montjoly
Intervalle inter-ponte (j)	28	13	10
Durée de la migration (an)	1-2	2-4	2-4

2. Le site de Rémire-Montjoly. Sur les plages de ce site, à 300 km à l'est de Yalimapo se trouve un deuxième site de ponte pour une autre population de tortues luths (Figure 1.16), génétiquement différente de la population de l'Ouest (Molfetti *et al.*, 2013). À l'inverse de la population de Yalimapo, celle de Rémire-Montjoly est en nette croissance, avec 2341 pontes recensées en 2005 et 3956 pontes en 2015 ONCFS. Bien que constituant pour cette espèce une part importante de son effectif dans l'Atlantique, aucun suivi satellitaire n'avait encore été réalisé sur cette population. Ce site de ponte abrite également une population de tortues olivâtres. Cette espèce est carnivore (*e.g.* poissons, crustacés, mollusques, méduses, Bjorndal 1997) et la plus petite des tortues marines, car elle mesure 70 cm et pèse environ 40 kg (`http://www.tortuesmarinesguyane.com/`) – Tableau 1.1. En Guyane française, la population de tortues olivâtre est en augmentation (1388 pontes recensées en 2005 *vs.* 3387 pontes recensées en 2015, ONCFS). Son statut UICN est vulnérable, et sa ponte a lieu tous les uns à deux ans, entre le mois d'avril et le mois de juillet. La tortue olivâtre est connue pour son impressionnante synchronisation au moment de la ponte, phénomène nommé *arribadas* (Plot *et al.*, 2012; Plotkin *et al.*, 1997; Pritchard, 1969). Il a lieu en moyenne tous les 28 jours en Guyane française (Plot *et al.*, 2012), moment au cours duquel les femelles vont pondre en

moyenne 110 œufs (Miller, 1997). Le suivi satellitaire de ses déplacements en migration post-ponte a permis d'identifier ses habitats d'alimentation, principalement situés sur le plateau des Guyanes (Plot *et al.*, 2015).

Bien que deux des trois espèces présentent en Guyane française aient déjà fait l'objet de nombreuses études portant sur le suivi satellitaire (Ferraroli *et al.*, 2004; Fossette *et al.*, 2012, 2008a, 2007, 2010a,b, 2014b; Georges *et al.*, 2007; Hays *et al.*, 2004a; Plot *et al.*, 2015, 2012), deux populations (sur les quatre nidifiant en Guyane) restaient encore à étudier, *i.e.* la population de tortues vertes de l'Ouest guyanais et celle de tortues luths de l'Est. Les travaux déjà publiés sur les déplacements des tortues luths et olivâtres de Guyane suggèrent une importante variabilité interspécifique en ce qui concerne les schémas de dispersion et le comportement de plongée. Il paraissait donc nécessaire de réaliser une étude comparative incluant le suivi satellitaire des trois espèces.

1.3.3 Le contexte océanographique du plateau des Guyanes

La région des Guyanes est une zone fortement dynamique, car à la fois sous l'influence de puissants courants océaniques et du panache amazonien. La conjugaison de ces deux facteurs génère des conditions océanographiques particulières pour les tortues marines.

La circulation océanique

La circulation de l'Atlantique tropical est bordée par les gyres subtropicales des deux hémisphères, qui incluent les courants équatoriaux nord (*North Equatorial Current*) et sud (*South Equatorial Current*, Didden & Schott, 1993; Lumpkin & Garzoli, 2005; Stramma *et al.*, 2003) – Figure 1.17.

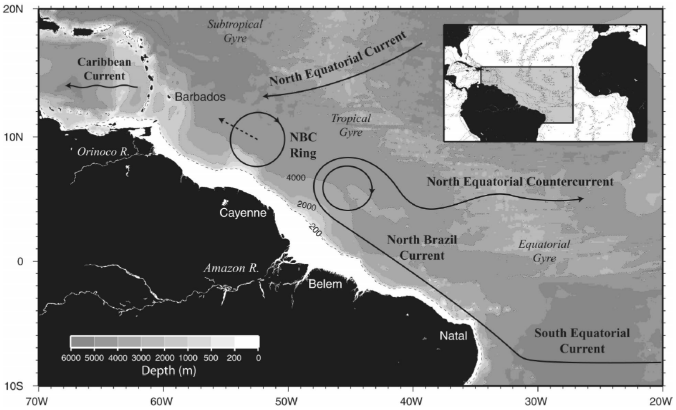


FIGURE 1.17 – Schéma de la circulation océanique des courants de surface de l'Atlantique tropical (issu de Fratantoni & Glickson 2002). NBC fait référence au courant nord-brésilien.

Le courant équatorial sud se dirige vers l'ouest le long de la côte brésilienne où il bifurque pour donner naissance au courant du Brésil vers le sud et au courant nord-brésilien (NBC) en direction de la Guyane française. Après avoir passé l'équateur, une partie du NBC continue sa course le long du plateau des Guyanes vers le nord-ouest, générant le courant des Guyanes, tandis que l'autre partie du NBC rétrofléchie à l'est en donnant naissance au contre-courant équatorial (*North Equatorial Countercurrent*), à approximativement 7 °N-48 °O (Figure 1.17). De puissants tourbillons anticycloniques (NBC *rings*) pouvant atteindre 400 km de diamètre sont générés dans cette zone de rétroflexion, et se propagent ainsi pendant plusieurs mois vers le nord-ouest (Didden & Schott, 1993; Fratantoni & Glickson, 2002; Fratantoni & Richardson, 2006; Wilson *et al.*, 2002).

L'influence du panache amazonien

Les structures tourbillonnaires générées par la rétroflexion du NBC transportent ainsi les eaux riches en nutriments originaires du fleuve Amazone (Baklouti *et al.*, 2007; Fratantoni & Glickson, 2002; Muller-Karger *et al.*, 1988). Le fleuve Amazone déverse 20% de l'eau douce mondiale qui rejoint les océans (Dagg *et al.*, 2004). Il contient le plus vaste bassin versant au monde et décharge annuellement jusqu'à 115.10^7 tonnes de sédiments et de matières en suspension dans l'Atlantique (DeMaster *et al.*, 1996; Meade, 1996; Milliman & Meade, 1983). Ces grandes quantités de sédiments rendent cette région extrêmement riche en chlorophylle *a*, et par conséquent très productive (DeMaster *et al.*, 1996; Fratantoni & Glickson, 2002; Muller-Karger *et al.*, 1988) – Figure 1.18.

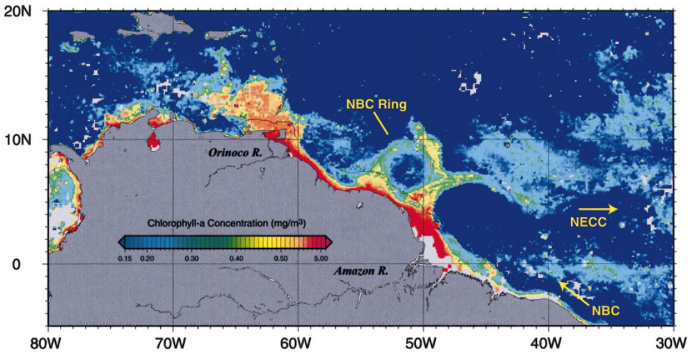


FIGURE 1.18 – Carte de la concentration en chlorophylle *a* montrant l'influence du panache amazonien et des tourbillons anticycloniques sur le plateau des Guyanes (issu de Fratantoni & Glickson 2002). NBC fait référence au courant nord-brésilien et NECC au contre-courant équatorial.

Dans ce contexte, le panache amazonien influence considérablement les conditions océanographiques et biogéochimiques du plateau des Guyanes, depuis la côte brésilienne jusqu'à la région caribéenne.

1.4 Problématique et structure de la thèse

1.4.1 Problématique

La Guyane française héberge donc pour leur reproduction trois des sept espèces de tortues marines présentes dans le monde (tortue olivâtre, tortue verte et tortue luth). Comme on l'a vu, elles sont réparties sur deux sites de ponte principaux, situés respectivement à l'ouest, sur la plage d'Awala-Yalimapo, et à l'est, sur la plage de Rémire-Montjoly. Nous avons aussi montré que par leurs traits d'histoire de vie ces trois espèces présentent des caractéristiques bien distinctes en termes de régime alimentaire, d'investissement énergétique lors de la ponte (durée de l'intervalle entre deux pontes successives, nombre d'œufs pondus et nombres de pontes par saison) et de durée de migration, ce qui a donc des conséquences sur leurs stratégies d'utilisation des ressources. De plus, nous avons mis en évidence la singularité du contexte océanographique du plateau des Guyanes, sous l'influence de puissants courants océaniques et du panache amazonien. Bien que depuis les années 2000 plusieurs femelles adultes gravides de tortues luths (Awala-Yalimpo) et de tortues olivâtres (Rémire-Montjoly) aient été suivies par satellite, à ce jour, aucune étude n'avait encore pris en compte l'influence de l'océanographie sur les déplacements de ces animaux dans les deux dimensions. Dans ce contexte, cette thèse vise donc à *étudier les déplacements de femelles adultes issues de ces trois espèces au cours de (A) l'inter-ponte et (B) durant la migration post-ponte, le tout en lien avec les structures océanographiques* dans la dimension horizontale (trajectoires) et verticale (comportement de plongée). Afin de relier le comportement de ces individus à leur environnement, nous avons déployé un total de 55 balises Argos entre 2012 et 2015 afin d'échantillonner à la fois le comportement des tortues (trajectoires et comportement de plongée) et leur environnement direct (température, salinité et fluorescence). Pour compléter ces données environnementales collectées *in situ*, une série de récents modèles prévisionnels de l'océan ont été utilisés, permettant la collaboration avec plusieurs laboratoires d'écologie et d'océanographie (nationaux et internationaux) tels que le LOCEAN (Paris), CLS (Toulouse), le CEFE (Montpellier), le CEBC (Chizé) ou encore le MISU (Université de Stockholm).

La forte hétérogénéité de l'écosystème marin va ainsi conditionner les déplacements des tortues marines, puisqu'elles doivent optimiser les habitats favorables à la ponte et à la prospection alimentaire. Or, puisque l'incubation des œufs dans le sol requiert une température tropicale, les meilleurs sites de ponte pour une espèce de tortue marine déterminée ne sont pas nécessairement les sites les plus appropriés pour l'optimisation de leur alimentation. *Les mouvements des tortues marines liés à chacune de ces activités sont donc déterminés par les conditions locales de chaque habitat*, *i.e.* un habitat pour se reproduire *vs.* un habitat pour s'alimenter. De telles conditions pousseraient ainsi ces animaux à initier des déplacements parfois sur plusieurs milliers de kilomètres et à des profondeurs importantes pour réaliser une activité bien spécifique pour trouver des congénères, se reproduire, pondre des œufs sur une plage propice à l'incubation, ou encore s'alimenter là où la ressource est disponible et abondante.

1.4.2 Structure de la thèse et objectifs

La structure de cette thèse s'articule donc autour du cycle de vie des tortues marines, *i.e.* saison de ponte et migration chez les femelles adultes. L'objectif est donc de comprendre ce qui détermine les déplacements en mer des tortues olivâtres, des tortues vertes et des tortues luths pendant (A) la saison d'inter-ponte et durant (B) la migration post-ponte (Figure 1.19). Ce manuscrit s'articule donc autour de ces deux parties (inter-ponte et migration post-ponte), dont les résultats sont présentés sous forme d'une synthèse, issue des six articles réalisés au cours des trois années de thèse. Pour chaque chapitre, les résultats portent sur les déplacements horizontaux et verticaux des trois espèces étudiées en lien avec leur habitat.

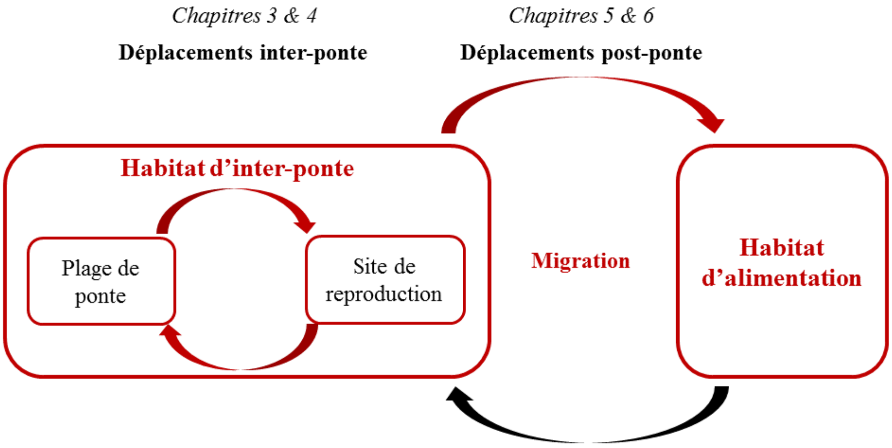


FIGURE 1.19 – Schéma représentatif de la structure du manuscrit de thèse présenté sous forme d'une synthèse en deux parties : (A) déplacements durant l'inter-ponte et (B) déplacements post-ponte. Les flèches rouges correspondent aux périodes étudiées au cours de cette thèse.

Chapitres 3 et 4 : les déplacements inter-ponte

Ces deux premiers chapitres portent sur les schémas de dispersion et le comportement de plongée des trois espèces en lien avec les structures océanographiques durant la saison d'inter-ponte. Cette première partie s'articule autour des deux sites de ponte de Guyane française :

- Chapitre 3 : le suivi des tortues vertes de l'Ouest guyanais (Annexe A),
- Chapitre 4 : le suivi des tortues olivâtres et des tortues luths de l'Est guyanais (Annexe B).

Chapitres 5 et 6 : les déplacements post-ponte

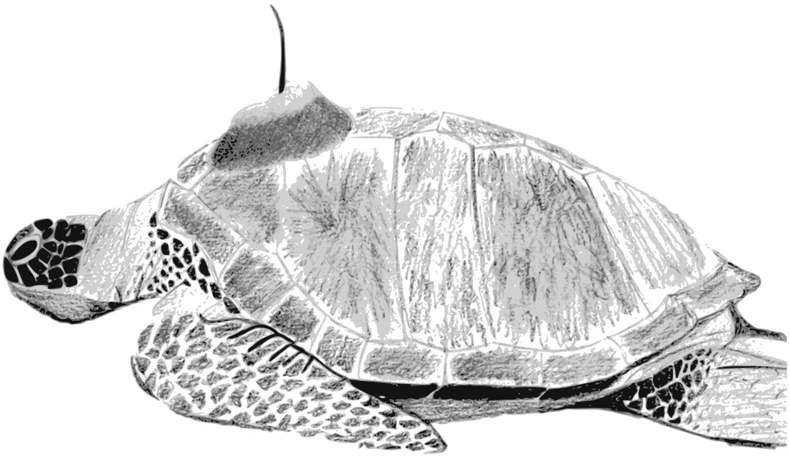
Les chapitres 5 et 6 portent sur la synthèse de quatre articles qui traitent des déplacements durant la migration post-ponte des trois espèces, en lien avec les facteurs océanographiques. Différentes méthodes ont été utilisées pour détecter les comportements de prospection alimentaire, ce qui a permis de caractériser les habitats d'alimentation. En accord avec le schéma de migration propre à chaque espèce, cette partie se décompose en deux axes :

- Chapitre 5 : la migration côtière des tortues vertes (Annexes D et E) et des tortues olivâtres (Annexe F),
- Chapitre 6 : la migration océanique des tortues luths (Annexe G).

CHAPITRE 2

Méthodologie

Sommaire



2.1 Suivis démographique et télémétrique

En plus du suivi télémétrique, un suivi démographique est réalisé tous les ans en Guyane française sur les trois espèces étudiées.

2.1.1 Suivi démographique

Depuis plus de 40 ans, un suivi démographique des tortues marines est réalisé sur les plages d'Awala-Yalimapo. Ce suivi consiste à identifier les tortues femelles gravides à l'aide de la méthode de Capture-Marquage-Recapture (CMR). Au cours de la saison de ponte, de février à juillet, des patrouilles nocturnes quotidiennes sont donc réalisées sur cette plage. Chaque tortue rencontrée est scannée à l'épaule (droite et gauche) à l'aide d'un lecteur manuel GR-250 (TROVAN®) pour vérifier si l'individu est marqué. Pour chaque tortue nouvellement rencontrée, l'individu est équipé d'un PIT (*Passive Integrated Transponder*) de type ID-100 BC (TROVAN®) placé respectivement dans le triceps droit pour la tortue verte et dans l'épaule droite pour la tortue luth. La taille de chaque individu est également mesurée à l'aide d'un mètre ruban souple, *i.e.* longueur et largeur curvilignes pour les trois espèces, ainsi que la circonférence pour les tortues luths. Sur la plage de Rémire-Montjoly, un suivi similaire est réalisé par l'association Kwata (`http://www.kwata.net/`).

Pour chaque individu rencontré, plusieurs paramètres sont collectés tels que la date, l'heure, l'espèce, le numéro PIT, la position GPS, le type de substrat (sable, bas de talus, haut de talus, végétation ou mer), le comportement (montée, premier balayage, creusement, ponte, rebouchage, deuxième balayage ou demi-tour). Toutes ces déterminations sont réalisées au moment de la ponte, afin de perturber le moins possible les individus. Le suivi démographique nous permet de connaître le nombre de pontes annuelles, le nombre de femelles observées chaque année, mais également de savoir à quelle fréquence les individus reviennent sur la plage (intervalle de migration et intervalle d'inter-ponte).

2.1.2 Déploiement des balises

Le protocole diffère selon que l'on équipe de balise Argos une tortue à écaille (tortue verte ou olivâtre) ou une tortue luth. La carapace des tortues à écailles permet une bonne fixation des balises à l'aide d'une colle forte (Epoxy®). En revanche, l'absence d'écaille chez la tortue luth et donc la présence d'un cuir ne permettent pas l'utilisation de cette colle ; un autre protocole est donc nécessaire.

Protocole pour les tortues à écailles

Après avoir vérifié la présence d'un PIT, ou après avoir inséré un PIT le cas échéant, un enclos en bois est placé autour de l'individu (tortue verte ou olivâtre) durant la phase d'oviposition (Figure 2.1, étape 1). Afin de retirer le sable et les épibiontes, (1) la dossière est ensuite nettoyée à l'aide d'un chiffon imbibé d'acétone, à l'endroit où la balise est fixée. La balise est ensuite (étape 2) positionnée le plus en avant possible de la carapace pour permettre une bonne transmission des données à chaque fois que la tortue remonte en surface pour respirer. Puis, (étape 3) la balise est fixée à l'aide d'une colle Epoxy®. Après un temps de séchage d'environ 2h, (étape 4) la tortue est relâchée et (étape 5) rejoint la mer.

FIGURE 2.1 – Principales étapes du déploiement d'une balise Argos sur une tortue olivâtre : (1) nettoyage de la carapace, (2) positionnement de la balise, (3) pose de la balise à l'aide de colle Epoxy®, (4) relâcher et (5) retour à la mer. Crédit photo : CNRS.

Protocole pour la tortue luth

Jusqu'à récemment, la méthode la plus utilisée pour déployer des balises satellites ou bio-loggers sur les tortues luths était de leur fixer un harnais sur l'animal (*e.g.* Eckert *et al.* 1986; Ferraroli *et al.* 2004; Fossette *et al.* 2007; Hughes *et al.* 1998). Toutefois, ce type de technique perturbe l'hydrodynamisme de la tortue en générant une importante force de traînée, mais aussi causer d'importantes blessures en raison du frottement du harnais sur la peau (Hawkins, 2004; Troëng *et al.*, 2006). De nouvelles techniques de fixation ont émergé, consistant à fixer la balise directement sur le cuir (*e.g.* Dodge *et al.* 2014;

Fossette *et al.* 2008a). En adaptant cette technique à la morphologie des tortues luths, D. Chevallier et la MIBE (Métrologie et Instrumentation en Biologie et Environnement) de Strasbourg ont conçu des moulages en résines sur lesquels sont insérées les balises. La zone de fixation de la balise, située au milieu de la carène centrale (Figure 2.2), est préalablement désinfectée avec de la Bétadine®. De la Lidocaïne® (anesthésiant) est ensuite injectée localement avant le perçage (deux trous d'un diamètre inférieur à 0,5 cm) de la carène centrale. Les balises sont ensuite fixées en passant un câble en acier inoxydable à travers les deux trous dans la carène et dans le moulage en résine. Le câble est ensuite sécurisé à l'aide de serre-câbles en acier inoxydable, puis recouvert de colle Epoxy® pour assurer la solidité et la protection du matériel (Figure 2.2).

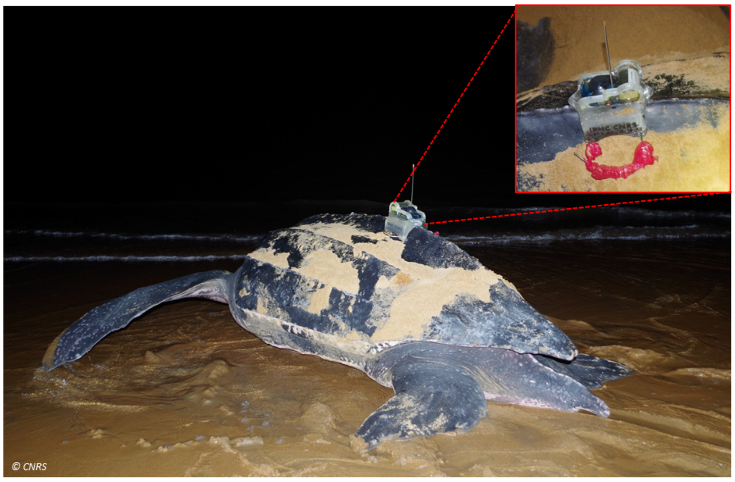


FIGURE 2.2 – Déploiement d'une balise Satellite Relay Data Logger (SRDL) sur une tortue luth à Rémire-Montjoly. Crédit photo : CNRS.

2.1.3 Données collectées

Entre 2012 et 2016, un total de 55 balises satellites a été déployé sur les trois espèces de tortues marines nidifiant en Guyane française (Tableau 2.1). Les 55 balises ont fourni des données en temps réel via le système Argos. Les données qui ont été fournies sont dites basse résolution, car correspondant à un résumé des plongées, *i.e.* une profondeur maximale par plongée, ou quatre profondeurs par plongée selon le type de balise. Les données haute résolution issues des balises Argos n'ont pu être récupérées. Jusqu'à présent, les tortues luths, dont la migration est pluriannuelle, sont revenues en Guyane française sans le matériel sur le dos. En deux à trois ans, les balises se décollent de la dossière et sont donc perdues avec leurs données haute résolution. Quatre modèles de balises provenant de deux constructeurs différents (Sea Mammal Research Unit et Wildlife Computers) ont donc été utilisés au cours de cette thèse.

Tableau 2.1 – Synthèse des balises analysées au cours de la thèse.

Année	Balise	Position	*n*	Site de déploiement	Espèce	Chapitre
2012	SPLASH-238A	Argos+GPS	16	Yalimapo	Verte	3 & 5
2013	SPLASH-296A	Argos+GPS	8	Rémire-Montjoly	Olivâtre	4 & 5
2013	CTD-Fluo-SRDL	Argos	2	Rémire-Montjoly	Olivâtre	4 & 5
2014	CTD-Fluo-SRDL	Argos	10	Yalimapo	Verte	3 & 5
2014	CTD-Fluo-SRDL	Argos	8	Rémire-Montjoly	Olivâtre	4 & 5
2014	SPLASH-238A	Argos+GPS	1	Rémire-Montjoly	Luth	4 & 6
2015	SRDL	Argos	10	Rémire-Montjoly	Luth	4 & 6

Les balises SPLASH10-F

Les balises SPLASH10-F sont conçues par Wildlife Computers^{TM} (Redmond, WA, États-Unis, `http://wildlifecomputers.com/`). Deux types de balises SPLASH10-F ont été déployées, à savoir les SPLASH10-F-238A (Figure 2.3a) sur les tortues vertes (*n* = 16 en 2012), et les SPLASH10-F-296A (Figure 2.3b) sur les tortues olivâtres (*n* = 8 en 2013) et une tortue luth en 2014 (Tableau 2.1). En plus de fournir la position de l'animal via le système Argos, ces balises ont été programmées pour également enregistrer les positions GPS des tortues via la technologie Fastloc GPS®.

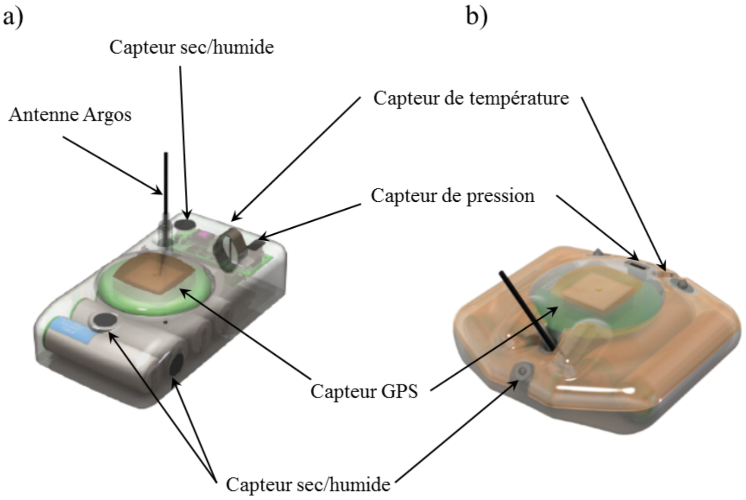


FIGURE 2.3 – Schémas d'une balise (**a**) SPLASH10-F-238A (10,5 x 5,6 x 3 cm, 217 g) et d'une balise (**b**) SPLASH10-F-296A (8,6 x 8,5 x 2,9 cm, 192 g). Images issues du site de Wildlife Computers.

Les données collectées par les balises sont transmises lorsque l'animal remonte en surface pour respirer. Ces deux types de balises enregistrent également des paramètres de plongée (profondeur maximale atteinte et durée de plongée, Figure 2.4a), et des données de température de l'eau. Seules les données basse résolution (données résumées) issues de ces balises ont pu être récupérées via le système Argos.

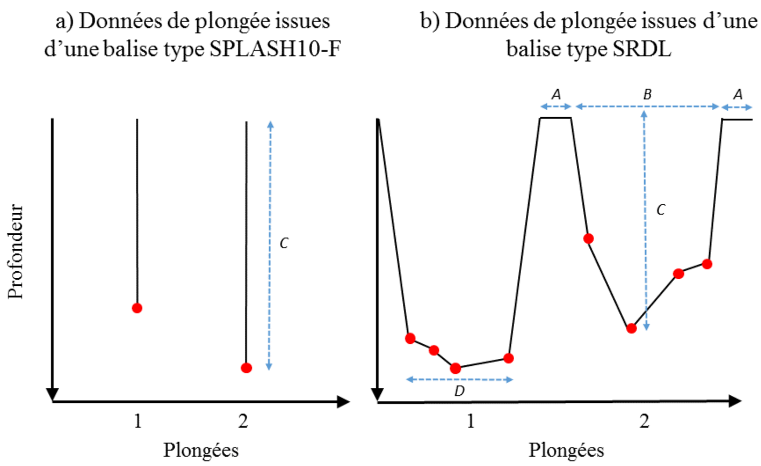


FIGURE 2.4 – Schéma des profils de plongées enregistrés par une balise (**a**) SPLASH10-F et une balise (**b**) SRDL avec quatre profondeurs (points rouges) par plongée. A : temps de surface, B : durée de la plongée, C : profondeur maximale de plongée, D : temps passé au fond (au-delà de 80% de la profondeur maximale de plongée).

Les balises SRDL

Les balises *Satellite Relay Data Logger* (SRDL) sont conçues par le Sea Mammal Research Unit™ (SMRU, Université de St Andrews, Écosse, `http://www.smru.st-and.ac.uk/Instrumentation/`). Deux types de balises SRDL ont été déployées, à savoir les 9000-SRDL (Figure 2.5a) sur des tortues luths en 2015 (n = 10) et les *Conductivity-Time-Depth-Fluorescence* SRDL (CTD-Fluo-SRDL, Figure 2.5b) sur des tortues vertes (n = 10) et olivâtres (n = 10, Tableau 2.1) entre 2013 et 2014.

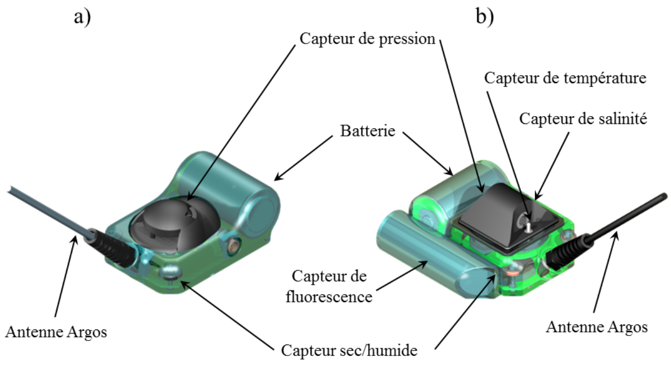


FIGURE 2.5 – Schémas d'une balise (**a**) 9000-SRDL (10,5 x 7 x 4 cm, 370 g) et d'une balise (**b**) CTD-Fluo-SRDL (11,5 x 10 x 4 cm, 680 g). Images issues du site du SMRU.

Comme les balises SPLASH10-F, les SRDL enregistrent la position de l'animal (mais uniquement via le système Argos), ainsi que des paramètres de plongée. À la différence des balises SPLASH10-F qui n'ont enregistré qu'une seule profondeur maximale atteinte concernant les données basse résolution, les balises SRDL ont, quant à elles, enregistré quatre profondeurs par plongée (plus les deux points en surface), ainsi que les temps de surface post-plongée (Figure 2.4b). Les CTD-Fluo-SRDL ont également la particularité de mesurer des variables océanographiques telles que la température (Figure 2.6a) et la salinité de l'eau (Figure 2.6b), ainsi que la fluorescence (utilisée comme un indicateur de la concentration en chlorophylle *a*, Figure 2.5b).

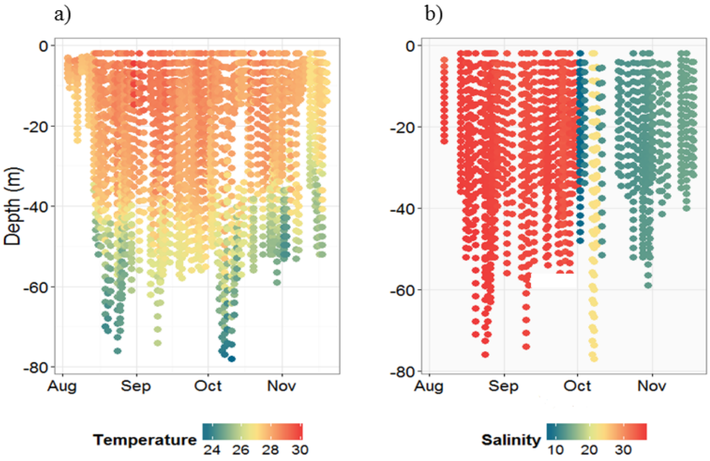


FIGURE 2.6 – Exemple de profils de (**a**) température (en °C) et de (**b**) salinité (en psu) enregistrés par une balise CTD-Fluo-SRDL déployée sur une tortue olivâtre en 2013 en Guyane française.

2.2 Analyses de données

2.2.1 Prétraitement des données

La majorité des balises a été déployée pendant la saison de ponte, ce qui a permis d'obtenir des données à la fois sur les déplacements en inter-ponte et en migration post-ponte. Une requête spatiale a donc été réalisée sous ArcGIS (version 10.1), afin d'identifier la date de départ en migration pour chaque individu, en se basant sur la distance journalière parcourue depuis le site de ponte et la dernière ponte réalisée (identifiée grâce aux capteurs sec/humide de la balise). Un filtre de vitesse a ensuite été appliqué à chaque trajectoire, en excluant les positions associées à une vitesse supérieure à 10 km.h^{-1} (Jonsen *et al.*, 2007b) pour les animaux en migration, et à 5 km.h^{-1} pour ceux en inter-ponte (Hays *et al.*, 2004a; Schofield *et al.*, 2013a). Après avoir extrait la bathymétrie correspondant à chaque position (depuis la base de données GEBCO, résolution 30 arc-sec, *i.e.* cellules de 1 km, `http://www.gebco.net/`), les localisations à terre (hors évènement de ponte) ont pu être supprimées. Enfin, toutes les positions associées à une classe de qualité Z ont été écartées des analyses, car pas assez précises. Les informations sur la méthodologie employée sont indiquées dans les articles situés en annexes (Annexes A, B, D, E, F et G).

2.2.2 Densités de Kernel et habitat en inter-ponte

Pour localiser et quantifier le domaine vital utilisé durant la période d'inter-ponte, la méthode des densités de Kernel (*Kernel density estimation*) a été employée et appliquée aux localisations Argos et GPS (Worton, 1989). Afin de minimiser l'autocorrélation spatiale, les positions journalières médianes ont été utilisées dans l'analyse des Kernels (Revuelta *et al.*, 2015; Schofield *et al.*, 2013a, 2010) – Figure 2.7.

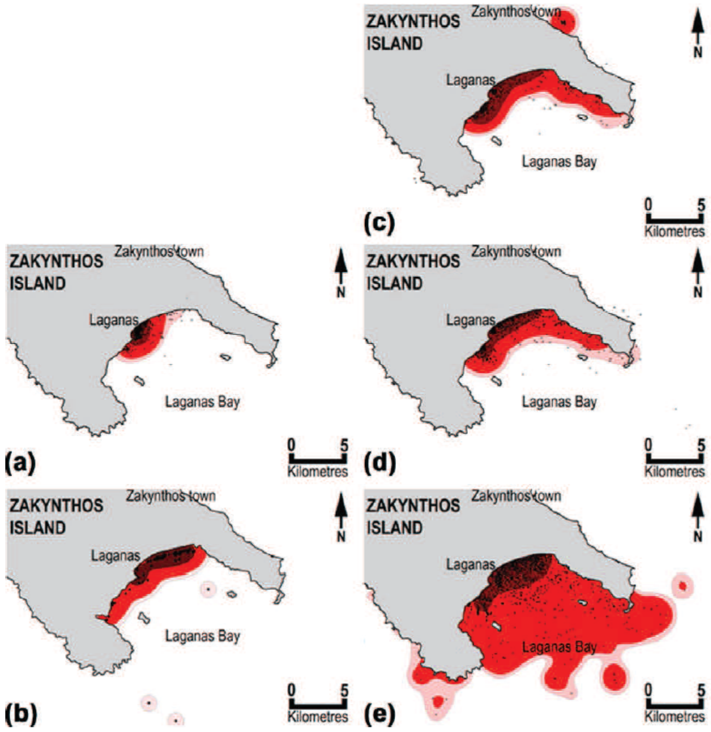


FIGURE 2.7 – Contours issus des densités de Kernel réalisées à partir des positions journalières médianes de tortues caouannes adultes suivies par balises Argos-GPS durant la période de reproduction en Méditerranée (issu de Schofield *et al.* 2010). (**a**) Quatre mâles suivis en 2007, (**b**) trois mâles suivis en 2008, (**c**) trois femelles suivies en 2006, (**d**) quatre femelles suivies en 2007 et (**e**) six femelles suivies en 2008.

Les surfaces associées aux contours à 50% (centre d'activité) et à 90% (domaine vital total) ont ensuite été calculées (Schofield *et al.*, 2010; Worton, 1989). La distance entre chaque position et le site de ponte et la distance à la côte ont également été calculées pour estimer la fidélité au site.

2.2.3 Identification de l'activité de prospection alimentaire

Lors du suivi pendant la migration post-ponte, l'objectif était tout d'abord d'identifier le comportement de prospection alimentaire afin de caractériser l'habitat utilisé en phase d'alimentation. Cette étape cruciale a donc été réalisée dans les deux dimensions, à commencer par le plan horizontal à partir des trajectoires.

Dans la dimension horizontale

Depuis une quinzaine d'années, un certain nombre de méthodes ont émergé pour permettre l'identification de ce que l'on appelle des zones de recherche restreinte (*Area-Restricted Search*, ARS). Parmi les nombreuses méthodes utilisées pour la détection de ces ARS dans le plan horizontal, le temps de premier contact (*First Passage Time* : FPT) a été initié par Fauchald & Tveraa (2003). Il consiste à calculer le temps nécessaire à un animal pour sortir d'un cercle virtuel de rayon *r* centré sur sa localisation (Figure 2.8a). L'hypothèse sous-jacente est qu'un long FPT correspond à des ARS, et par conséquent, à de potentiels évènements de prospection alimentaire. L'extension du FPT développée par Barraquand & Benhamou (2008) est le temps de résidence (*Residence Time* : RT). Le RT associé à une localisation donnée correspond au FPT, auquel on cumule le temps de passage dans le cercle qui a eu lieu avant et après avoir la position considérée (Figure 2.8b). Ces deux méthodes ont ainsi été employées dans les trois articles de cette thèse qui portent sur les déplacements en migration post-ponte (Annexes E, F et G).

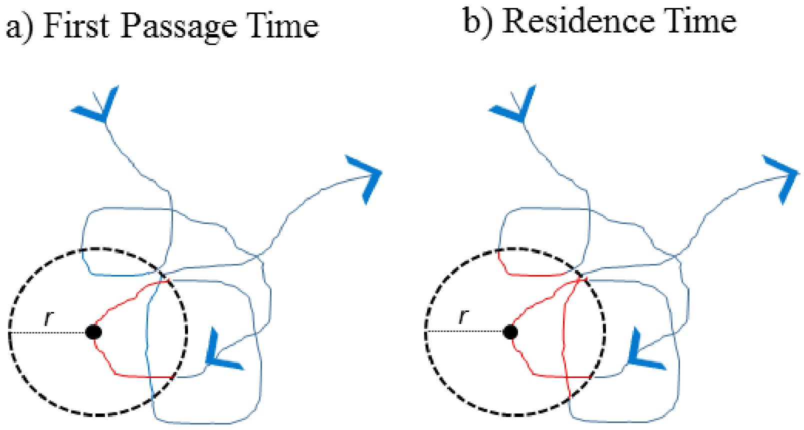


FIGURE 2.8 – Schéma de la méthode du First Passage Time (**a**) et du Residence Time (**b**) pour identifier les zones de recherche restreinte (ARS). Inspiré de Barraquand & Benhamou 2008.

Dans la dimension verticale

La forme des plongées peut également être un indicateur de l'activité réalisée par l'animal, *i.e.* alimentation, transit ou repos (Le Boeuf *et al.*, 2000; Hindell *et al.*, 1991;

Schreer *et al.*, 2001). En effet, les plongées en « V » sont considérées comme des plongées exploratoires ou de transit (Figure 2.9a), tandis que les plongées en « U » sont généralement synonymes de repos ou de prospection alimentaire centrés sur le fond de la plongée (Figure 2.9b). Pour chaque plongée résumée fournie par les balises de type SRDL, le *Time of Allocation at Depth* (TAD) a été calculé afin d'obtenir une estimation de la forme des plongées (Fedak *et al.*, 2001).

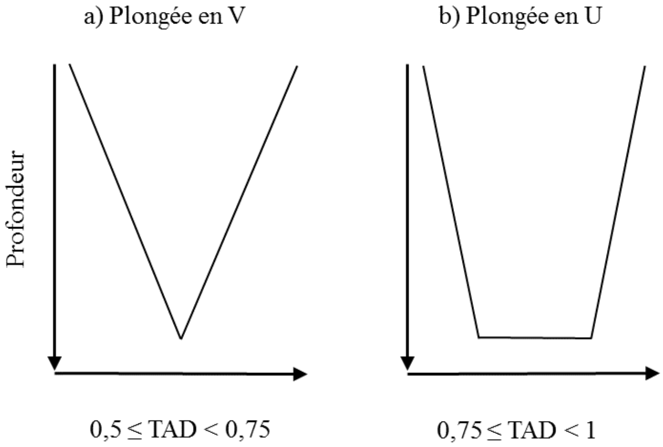


FIGURE 2.9 – Schéma représentant les deux formes de plongées les plus courantes en fonction de leur TAD : (**a**) plongée en V et (**b**) plongée en U.

De manière schématique, une plongée classique peut être caractérisée par quatre phases principales : la descente, la phase de fond, la remontée et la surface. À partir des données de plongée résumées issues des balises SRDL, le temps passé dans la phase de fond a ainsi pu être identifié comme le temps passé au-dessous de 80% de la profondeur maximale de plongée (Schreer *et al.*, 2001; Lesage *et al.*, 1999). Une plongée avec une longue phase de fond est généralement associée à une activité de prospection alimentaire (Schreer *et al.*, 2001). De nombreuses études ont notamment confirmé cette théorie chez les prédateurs plongeurs tels que l'éléphant de mer austral (*e.g.* Bailleul *et al.* 2008; Dragon *et al.* 2010) ou encore les oiseaux marins (Chappell *et al.*, 1993; Tremblay & Cherel, 2000; Schreer *et al.*, 2001), qui concentrent leur activité de prospection alimentaire dans la phase de fond. Toutefois, selon l'espèce considérée et la structure de l'environnement océanographique, l'activité de prospection alimentaire peut avoir lieu en dehors de ces phases de fond (Heerah *et al.*, 2014). Afin de suivre cette récente approche, nous avons utilisé une méthode développée par Heerah *et al.* (2014), *i.e.* le temps de chasse (*hunting time*) sur les phoques de Wedell et les éléphants de mer, et qui consiste à identifier les ARS au sein des plongées grâce à l'augmentation de la sinuosité verticale (Heerah *et al.*, 2014).

Les auteurs ont démontré que les phases de chasse (ARS verticales, Figure 2.10a) associées à une sinuosité verticale plus importante présentaient un nombre de tentatives de captures de proies plus élevé. En fixant un seuil de sinuosité verticale, ils ont donc pu discriminer deux phases : transit et prospection alimentaire (Figure 2.10a) à l'aide de l'indice de chasse $hunting_{highres}$. Cependant, sachant que la sinuosité verticale ne peut être calculée à partir des données basses résolution (l'essentiel des données traitées au cours de cette thèse), Heerah *et al.* (2015) ont développé un indice de chasse basse résolution ($hunting_{lowres}$), basé sur la vitesse verticale, *i.e.* le taux de variation exprimé en m.s^{-1} entre les profondeurs enregistrées par les balises SRDL (Figure 2.10b).

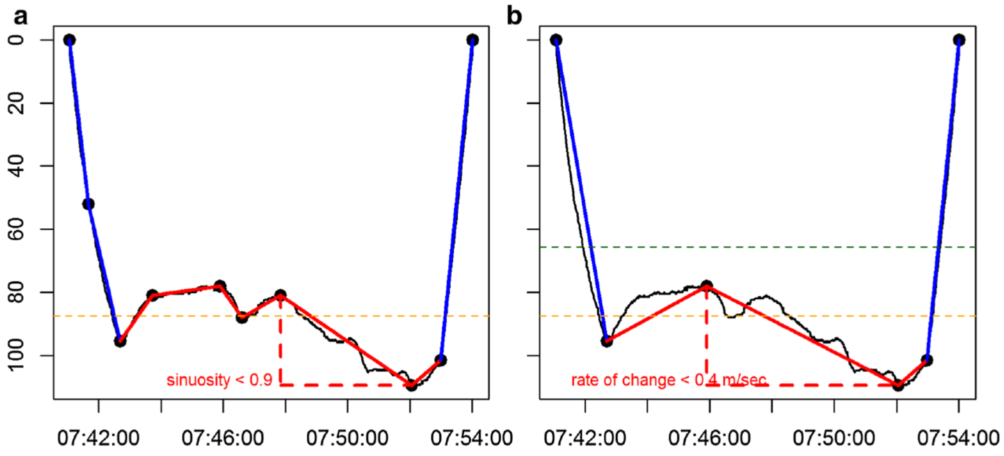


FIGURE 2.10 – Schéma illustrant deux plongées (**a** : haute résolution et **b** : basse résolution résumées par quatre profondeurs) enregistrées par une balise CTD-SRDL déployée sur un phoque de Wedell (issu de Heerah *et al.* 2015). Les segments en bleu représentent les phases de transit, tandis que les segments en rouge représentent (**a**) le $hunting_{highres}$ (temps de chasse haute résolution associé à une sinuosité verticale $\leq$ 0,9), et (**b**) le $hunting_{lowres}$ (temps de chasse basse résolution, segments associés à une vitesse verticale $\leq 0,4\ m.s^{-1}$).

Cette deuxième méthode a donc été adaptée aux tortues marines suivies au cours de cette thèse, en particulier aux tortues olivâtres, afin d'identifier à quelle profondeur cette espèce est susceptible de chasser durant la migration, et surtout quelle est la proportion du temps de chasse par rapport à la durée totale de chaque plongée. Pour plus de détail concernant cette approche, se référer à l'annexe F. Cette technique n'a pas pu être appliquée aux tortues vertes en raison de leur comportement essentiellement benthique au cours de l'alimentation, puisqu'elles se nourrissent d'herbiers ou d'algues marines. Concernant la tortue luth, son comportement de plongée particulier en migration (majorité de plongées en V) a rendu difficile et peu fiable l'utilisation du temps de chasse sur cette espèce.

2.2.4 Variables environnementales utilisées

Afin de relier le comportement de prospection alimentaire aux caractéristiques locales de l'habitat (physiques et biologiques), un certain nombre de variables environnementales ont été extraites à partir de différentes bases de données internationales (Tableau 2.2).

Les variables de surface

Les variables physiques telles que les *courants*, ont permis de calculer la vitesse de nage réelle des tortues, mais également de savoir si elles se déplacent ou non dans le sens du courant. Les données de courants ont également permis de corriger les trajectoires des individus, et ainsi d'identifier les ARS 'réelles', et non les ARS induites par un animal luttant contre le courant (Gaspar *et al.*, 2006). La *température de surface* (*SST*, issue de Copernicus-MyOcean, `http://marine.copernicus.eu/`) permet de connaître les amplitudes thermiques recherchées par les tortues marines. Cette variable peut affecter leur comportement, mais également la distribution de leurs proies. La *hauteur d'eau* a été utilisée pour identifier les zones tourbillonnaires, mais aussi les zones frontales en calculant le gradient de hauteur d'eau (idem pour la SST). Le modèle de *Finite-Size Lyapunov Exponents* (FSLE) fourni par le LOCEAN a également été utilisé pour localiser les zones de fronts, notamment dans l'étude des déplacements migratoires de la tortue luth. Concernant la tortue verte qui est herbivore à l'âge adulte et dont la ressource principale (herbiers et algues marines) est dépendante de la lumière qui pénètre dans la colonne d'eau, le *coefficient d'atténuation de la lumière* (un indicateur de la turbidité de l'eau) a donc été utilisé.

Concernant les variables biologiques, communément utilisées comme indicateurs de la concentration en proies, différents niveaux trophiques ont été utilisés, *i.e.* la concentration en chlorophylle *a* et la biomasse de micronecton. Le micronecton comprend tous les organismes planctoniques se déplaçant librement dans la colonne d'eau et mesurant entre 2 et 25 cm, *e.g.* méduses, crustacés, céphalopodes ou poissons (Lehodey *et al.*, 2008). La biomasse de micronecton est prédite par le modèle SEAPODYM (*Spatial Ecosystem And POpulation DYnamics Model*) et permet d'estimer la biomasse de proies potentielles des tortues olivâtres et des tortues luths, pour mieux expliquer leurs déplacements en migration. Le micronecton est modélisé à partir de données de courants et de température (fournies par le produit GLORYS-2v1) de la production primaire et la couche euphotique dérivées des données satellitaires à partir du modèle VGPM (*Vertically Generalised production Model*, `http://www.science.oregonstate.edu/ocean.productivity/`).

Tableau 2.2 – Variables environnementales utilisées au cours de la thèse.

Variable	**Unité**	**Résolution spatiale (° décimal)**	**Résolution temporelle**	**Produit**	**Source**
Bathymétrie	m	0,009	-	GEBCO	GEBCO
Courants océaniques	m.s^{-1}	0,08	Journalière	PHYS 001-024	Copernicus
Température de surface de l'eau	°C	0,08	Journalière	PHYS 001-024	Copernicus
Hauteur d'eau	cm	0,08	Journalière	PHYS 001-024	Copernicus
Coefficient d'atténuation de la lumière	m^{-1}	0,03	Mensuelle	MODIS Aqua	Oceancolor
Filaments et fronts	jour^{-1}	0,08	Journalière	FSLE	LOCEAN
Concentration en chlorophylle *a*	mg.m^{-3}	0,5	Hebdomadaire	BIO 001-014	Copernicus
Biomasse de micronecton	g.m^{2}	0,25	Hebdomadaire	SEAPODYM	CLS
Profondeur euphotique	m	0,25	Hebdomadaire	SEAPODYM	CLS
Température de l'eau	°C	0,25	Journalière	PHYS 001-024	Copernicus
Salinité de l'eau	psu	0,25	Journalière	PHYS 001-024	Copernicus
Profondeur de la couche de mélange	m	0,25	Journalière	PHYS 001-024	Copernicus
Concentration en chlorophylle *a*	mg.m^{-3}	0,5	Hebdomadaire	BIO 001-014	Copernicus

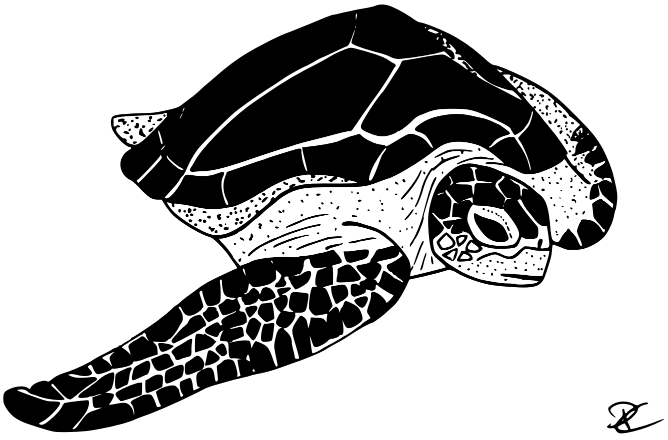
Les variables dans la colonne d'eau

Dans la colonne d'eau, les mêmes variables que celles extraites en surface ont permis de calculer de nouveaux paramètres pour caractériser les structures océanographiques verticales, et ainsi relier le comportement de plongée des tortues marines à ces structures verticales. Ainsi, l'extraction de la température et de la salinité de l'eau a permis d'identifier la profondeur de la *thermocline* (zone de fort gradient thermique) et celle de la *halocline* (zone de fort gradient de salinité). De la même manière, la profondeur de la *nutricline* (zone de maximum de chlorophylle *a*) a été identifiée à partir des données de chlorophylle *a* extraites à différentes profondeurs. Enfin, la profondeur de la couche de mélange, qui est un produit récemment développé par Copernicus-MyOcean, a été utilisée pour identifier les couches productives, riches en nutriments (Tableau 2.2).

CHAPITRE 3

Déplacements inter-ponte : l'Ouest guyanais

Sommaire



Ce troisième chapitre porte sur les déplacements en inter-ponte des tortues vertes de l'Ouest guyanais, suivies depuis les sites de Galibi et d'Awala-Yalimapo. Cette première partie des résultats est la synthèse d'un article publié dans *Marine Ecology Progress Series* (Annexe A).

3.1 Contexte et hypothèse

Afin d'économiser de l'énergie durant la saison de reproduction, les tortues marines ont su développer différentes stratégies telles que le repos sur le fond marin (Hays *et al.*, 2000; Houghton *et al.*, 2008; Sakamoto *et al.*, 1993; Walcott *et al.*, 2013; Houghton *et al.*, 2002; Reina *et al.*, 2005), entre deux eaux en contrôlant leur flottabilité (Minamikawa *et al.*, 1997; Hays *et al.*, 2000), en surface (phénomène de *basking*), ou encore en limitant leurs déplacements en restant proches de leur site de ponte (Stoneburner, 1982; Hays *et al.*, 1999; Blanco *et al.*, 2013; Maxwell *et al.*, 2014; Esteban *et al.*, 2015). Les tortues marines peuvent également s'alimenter lorsque les ressources sont disponibles sur les habitats de reproduction (Hays *et al.*, 2002b; Schofield *et al.*, 2006; Georges *et al.*, 2007). C'est le cas notamment à Chypre, où des tortues vertes ont été observées en train de s'alimenter dans des herbiers durant l'inter-ponte (Hays *et al.*, 2002b). Dans l'Ouest guyanais, l'importante population de tortues vertes (Schulz, 1975; Chevalier *et al.*, 1998) n'a encore jamais fait l'objet d'un suivi télémétrique au cours de cette saison d'inter-ponte. Rappelons que cette période induit un investissement énergétique important, notamment durant l'oviposition, obligeant ainsi les individus à développer une stratégie de reproducteur sur capital ou de reproducteur sur revenu (Chapitre 1). Les eaux du plateau continental contiennent d'importantes quantités de sédiments et de particules en suspension qui sont déversées continuellement par l'Amazone et les fleuves de Guyane française (le Maroni et la Mana, Milliman & Meade 1983; DeMaster *et al.* 1996; Lambs *et al.* 2007; Jounneau & Pujos 1988), générant des eaux turbides et saumâtres, peu propices au développement d'herbiers. On s'attendait par conséquent à ce que *la tortue verte de Guyane française adopte durant l'inter-ponte une stratégie de reproducteur sur capital en économisant ses réserves énergétiques, e.g. en limitant ses déplacements et en réalisant majoritairement des plongées benthiques de repos.*

3.2 Méthodologie

Les résultats de ce troisième chapitre sont issus du suivi satellitaire de 26 femelles adultes tortues vertes équipées depuis la Réserve Naturelle de Galibi au Suriname (n = 8) et la Réserve Naturelle de l'Amana sur la plage d'Awala-Yalimapo en Guyane française (n = 18) :

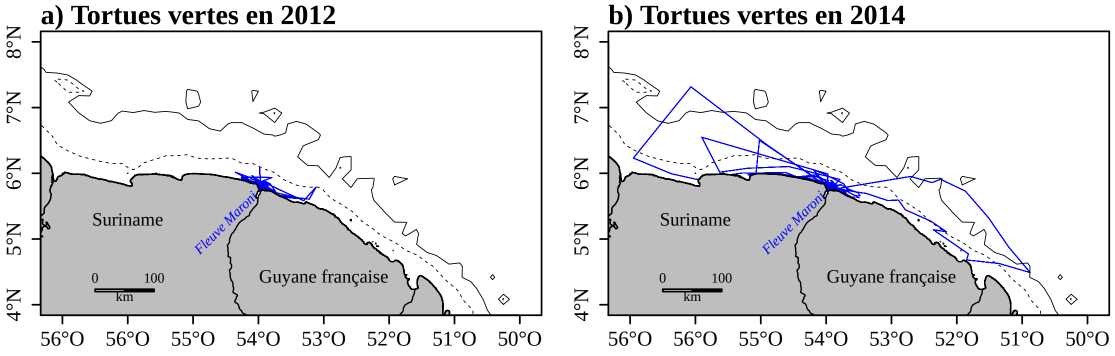
- Seize tortues vertes équipées en 2012 de balises SPLASH10-F-238A ;

- Et dix tortues vertes équipées en 2014 de balises CTD-Fluo-SRDL.

Pour estimer la surface du domaine vital utilisé par la tortue verte en inter-ponte, la méthode des densités de Kernel a été utilisée à partir des positions (Argos et GPS) médianes journalières. Enfin, les informations de *haulout* fournies par les balises via le capteur sec/humide ont été utilisées pour identifier les temps de surface prolongés (*Extended Surface Time*, ESTs, Hochscheid *et al.* 2010) associés à un comportement de repos en surface (*basking*). Chaque *haulout* est enregistré après 20 min consécutives en mode "sec" pour les balises SPLASH10-F, tandis que pour les CTD-Fluo-SRDL, un *haulout* est enregistré après 10 min. Sachant que les tortues vertes de Guyane française pondent essentiellement la nuit, tous les haulout enregistrés durant la journée ont été considérés comme des ESTs. La méthodologie employée est détaillée dans l'Annexe A. Pour le comportement de plongée, nous n'aborderons que les résultats issus des dix balises CTD-Fluo-SRDL déployées en 2014 (1237 profils de plongée résumés), qui ont fourni une meilleure résolution comparée aux balises SPLASH10-F (pour les résultats issus des SPLASH10-F se référer à l'Annexe A).

3.3 Trajectoires

La durée du suivi en inter-ponte a varié de 4 à 95 j (disponible depuis `www.int-res.com/articles/suppl/m555p235supp.pdf`). Les individus ont parcouru des distances plus importantes en 2014 qu'en 2012 (867,4 ± 714,6 km *vs.* 648,2 ± 310,6 km, respectivement), ce qui témoigne d'une variabilité interannuelle d'une cohorte à l'autre. En 2014, deux tortues ont réalisé deux boucles au large de la Guyane française et du Brésil,dans le sens du puissant courant des Guyanes, tandis que les huit autres sont restées à proximité de leur plage de ponte (Figure 3.1).



a) Tortues vertes en 2012

b) Tortues vertes en 2014

FIGURE 3.1 – Trajectoires des tortues vertes durant l'inter-ponte en 2012 (**a**, n = 15) et en 2014 (**b**, n = 10). La ligne en pointillées délimite l'isobathe des 20 m et la ligne pleine l'isobathe des 100 m. SUR désigne le Suriname et GF la Guyane française.

Ce comportement pourrait expliquer une partie de cette variabilité interannuelle, qui peut aussi être liée à un manque d'expérience des individus ou encore à des conditions environnementales différentes d'une année sur l'autre (érosion de la plage de Yalimapo, accrétion du banc de base en face du fleuve Maroni, etc.). Toutefois, un suivi sur le plus long terme en équipant davantage d'individus est nécessaire pour confirmer une telle tendance. Pour les deux années confondues, la distance moyenne à la côte (± SD) a été de 3,8 ± 3,1 km, et la distance à la plage de ponte de 18,6 ± 22,7 km. Ces résultats concordent avec la forte fidélité au site de ponte, qui a déjà été documentée chez les tortues marines durant l'inter-ponte (Schofield *et al.*, 2010; Hays *et al.*, 2014).

3.4 Surface des domaines vitaux

Une grande différence dans l'utilisation de l'habitat a été observée entre les deux années. En 2012, le domaine vital (Kernel à 90%) a occupé une surface de 351,3 km², pour un centre d'activité de 89,9 km² (Kernel à 50%, Figure 3.2a), tandis qu'en 2014, la superficie du domaine vital a été jusqu'à 42 fois supérieure (15050 km²), avec un centre d'activité occupant 1620,8 km² (Figure 3.2b). Cette variabilité interannuelle semble en partie expliquée par les déplacements très extensifs de deux individus suivis en 2014 comparés à ceux des autres tortues vertes qui sont restées beaucoup plus proches du site de ponte. Le faible domaine vital occupé coïncide avec le comportement d'inter-ponte observé chez les tortues vertes de Floride (Hart *et al.*, 2013), ou encore du Pacifique (Blanco *et al.*, 2013), et suggère une stratégie mise en place pour favoriser l'allocation d'énergie à l'oviposition en limitant les déplacements.

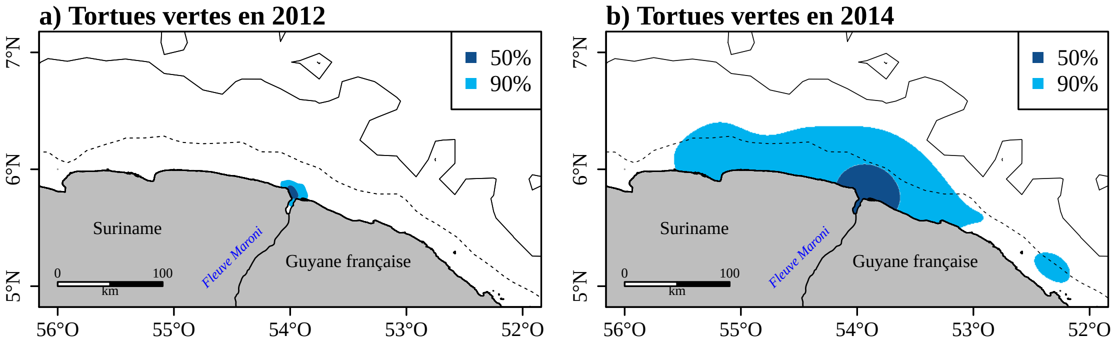


FIGURE 3.2 – Contours issus des densités de Kernel (90% en turquoise et 50% en bleu foncé) des tortues vertes suivies en 2012 (**a**, n = 15) et 2014 (**b**, n = 10). La ligne en pointillés délimite l'isobathe des 20 m et la ligne pleine l'isobathe des 100 m.

3.5 Comportement de plongée

La profondeur maximale atteinte (± SD) a été de 2,6 ± 2,1 m (min-max : 1,5-32 m), et 59% des plongées ont été réalisées dans les deux premiers mètres (Figure 3.3a). La profondeur maximale de plongée a été significativement différente d'un individu à l'autre (test de Kruskal-Wallis : p < 0,001). Cette variabilité interindividuelle pourrait être liée aux différences de condition corporelle ou encore aux conditions océanographiques rencontrées (Gaspar *et al.*, 2006). Le manque de données océanographiques collectées en 2012 ne permet toutefois pas d'étayer cette hypothèse, c'est pourquoi une nouvelle campagne de déploiement de balises CTD-SRDL s'avère nécessaire pour confirmer cette tendance.

Les plongées ont duré en moyenne (± SD) 4,0 ± 4,7 min (min-max : 0,5-35 min), et 79% des plongées ont duré moins de 5 min (Figure 3.3b). La durée des plongées a varié significativement d'un individu à l'autre (test de Kruskal-Wallis : p < 0,001).

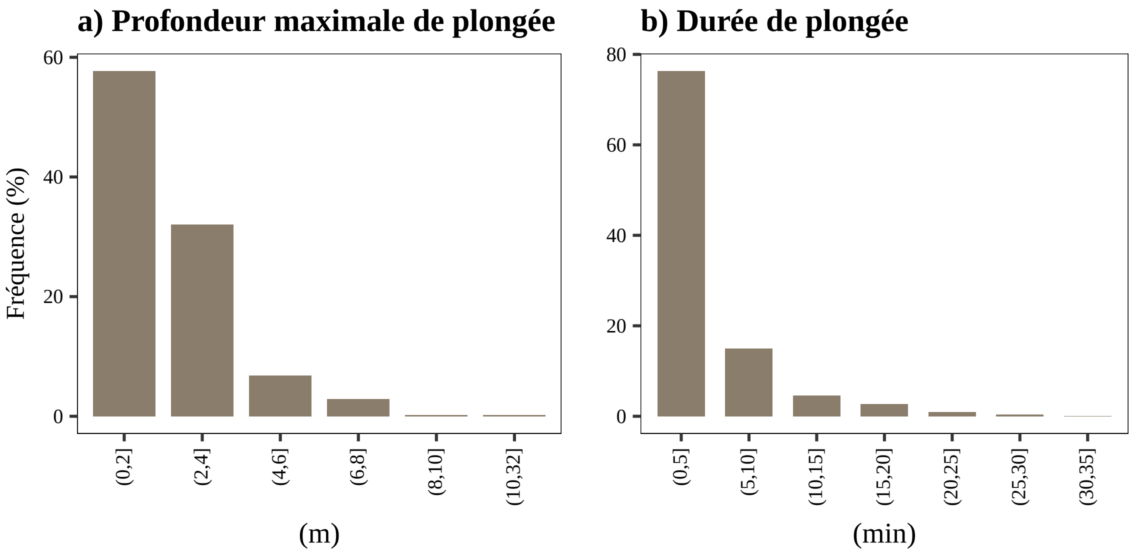


FIGURE 3.3 – Histogrammes de la profondeur maximale atteinte (**a**) et de la durée de plongée (**b**) enregistrées par les dix balises CTD-Fluo-SRDL déployées sur les tortues vertes à Awala-Yalimapo en 2014.

Un comportement similaire a été observé chez les tortues vertes du Costa Rica (69% des plongées < 5 m et 72% entre 2-10 min, Blanco *et al.* 2013) et les tortues luths d'Awala-Yalimapo en Guyane française (59% des plongées < 5 m et 60% < 6 min, Fossette *et al.* 2007). Pour qu'une tortue verte adulte de taille moyenne (109-127,7 cm de longueur de carapace curviligne) atteigne la flottabilité neutre et donc économise de l'énergie en plongée (phase de repos), il a été démontré qu'elle doit plonger à 19 m avec les poumons remplis d'air (Hays *et al.*, 2000). Les individus étudiés dans le cadre de cette thèse ayant une taille similaire, on suppose que les très faibles durées de plongées enregistrées par nos individus pourraient être dues à l'impossibilité d'atteindre la flottabilité neutre pour se reposer. Autre possibilité, dans ces eaux a priori dépourvues d'herbiers marins, les tortues vertes adultes pourraient se nourrir de crustacés, d'invertébrés ou de cnidaires présents dans ces eaux (Bjorndal, 1982; González Carman *et al.*, 2012; Santos *et al.*, 2015).

Concernant la forme des plongées, 43% étaient en U (TAD > 0,75) et 47% en V (0,5 < TAD < 0,75). Les tortues vertes ont majoritairement réalisé des plongées benthiques (62% *vs.* 38% pélagiques, bathymétrie-profondeur maximale atteinte > 1 m) - Annexe A, Figure 4. Les plongées en U benthiques sont typiques chez cette espèce et suggèrent soit une activité de prospection alimentaire sur le fond (Hochscheid *et al.*, 1999; Hays *et al.*, 2002b), ou bien une activité de repos comme cela a été démontré chez les tortues vertes de l'île d'Ascension (Hays *et al.*, 2000, 2002b). Il est nécessaire de collecter les données haute résolution pour pouvoir identifier le type d'activité réellement réalisé par ces tortues vertes en inter-ponte.

Le nombre moyen (± SD) de temps de surface prolongés (ESTs) a été de 13,6 ± 9,5 ESTs par femelle (min-max : 3-29 par individu). La durée des ESTs a été longue puisque les femelles ont passé en moyenne (± SD) 210 ± 288 min en ESTs (min-max : 10-1920 min). À la différence des tortues vertes du Pacifique, ces ESTs suggèrent un comportement de repos le jour (*basking*, en surface ou sur le sable), qui est renforcé par l'observation directe de tortues vertes se reposant sur le banc de sable situé à l'embouchure du fleuve Maroni (Chevallier D., communication personnelle). La faible bathymétrie associée à la flottabilité positive des tortues vertes rendent probablement le repos en surface plus profitable que le repos au fond de l'eau. Un tel comportement de *basking* peut aussi s'avérer bénéfique pour la thermorégulation (Sapsford & Van der Riet, 1979; Hochscheid *et al.*, 2010), pour éviter des mâles agressifs ou de potentiels prédateurs (Swimmer *et al.*, 2006), ou encore pour limiter les attaques fongiques (Boyer, 1965; Swimmer *et al.*, 2006).

3.6 Conditions océanographiques variables

En 2014, les balises CTD-Fluo-SRDL ont collecté 57 profils de température-salinité contenant 516 enregistrements. La salinité moyenne (± SD) a été de 24,6 ± 10,3 psu (min-max : 1,2-35,5 psu), et la température moyenne (± SD) de 26,8 ± 0,5 °C (min-max : 25,3-28,4 °C) - Figure 3.4. Ces eaux turbides et ces conditions de salinités très variables résultent des effets conjugués des marées (Lam-Hoai *et al.*, 2006), des précipitations (2000 à 4000 mm.an^{-1}, Lambs *et al.* 2007) et des fleuves situés à proximité du site de ponte (la Mana, le Maroni et l'Amazone, Jounneau & Pujos 1988; Froidefond *et al.* 2002). Les tortues vertes de Guyane française ont donc traversé des eaux très variables, allant d'un habitat oligohalin (< 5 psu) à ultrahalin (> 35 psu), montrant ainsi une tolérance élevée à des habitats contrastés. L'amplitude des températures (23-33 °C) a été légèrement plus grande que celle enregistrée par leurs congénères de l'Atlantique (27-28 °C, Hays *et al.* 2002a) et du Pacifique (27-29 °C, Blanco *et al.* 2013). Cette différence est probablement liée aux apports d'eaux douces (plus chaudes) provenant des fleuves Maroni et Mana (Nikiema *et al.*, 2007).

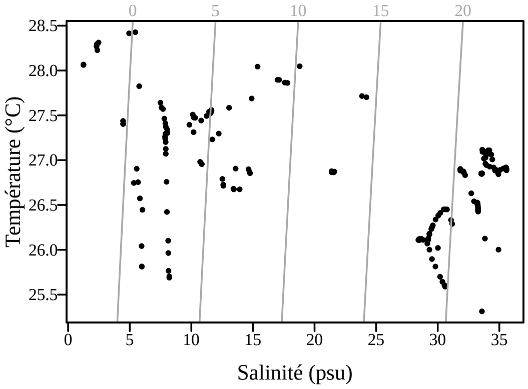


FIGURE 3.4 – Diagramme Température-Salinité issu des balises CTD-Fluo-SRDL de 2014. Les lignes et les nombres en gris représentent les isopygnes et les valeurs de densité de l'eau (exprimées en kg.m^{-3}).

3.7 Résumé

Le suivi satellitaire des tortues vertes de Guyane française durant la saison d'inter-ponte a permis d'estimer leur domaine vital, de caractériser cet habitat estuarien situé à l'embouchure du fleuve Maroni et d'étudier leur comportement de plongée. Ces résultats montrent :

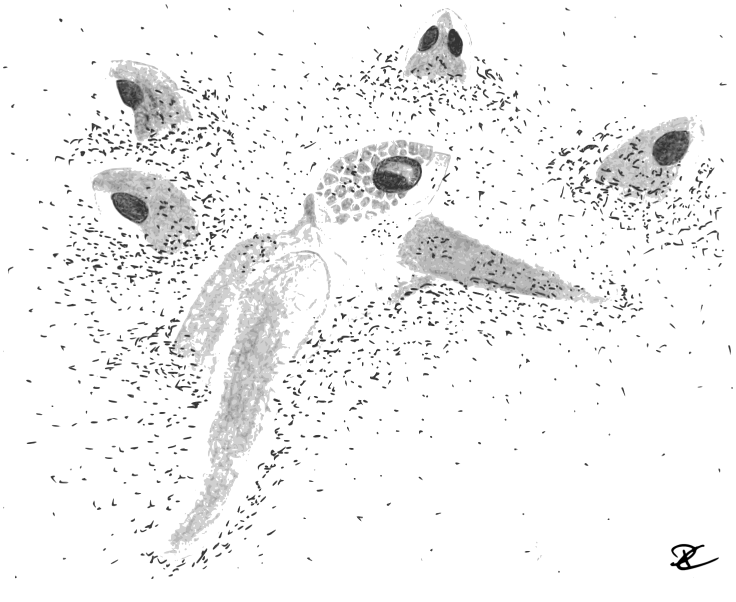
- Un domaine vital qui peut varier considérablement d'une année sur l'autre (89,9 km² en 2012 *vs.* 1620,8 km² en 2014), reflétant une possible différence de conditions environnementales et d'expérience des individus.
- Une forte fidélité au site de ponte avec une distance à la plage de ponte faible (18,6 ± 22,7 km).
- Des conditions de salinité très variables (min-max : 1,2-35,5 psu) car sous l'influence de plusieurs fleuves (le Maroni et la Mana).
- Des plongées majoritairement benthiques, brèves (79% des plongées < 5 min) et peu profondes (59% < 2 m), synonymes de repos au fond ou de prospection alimentaire.
- Un comportement de repos en surface ou à terre durant la journée.

À la différence des tortues vertes qui semblent privilégier un comportement passif pour économiser de l'énergie durant l'inter-ponte, les tortues olivâtres et les tortues luths de l'Est guyanais adoptent plutôt un comportement actif, réalisant différentes activités durant cette période (Chapitre 4).

CHAPITRE 4

Déplacements inter-ponte : l'Est guyanais

Sommaire



Ce quatrième chapitre concerne la synthèse d'un article publié dans *Journal of Marine Systems* (Annexe B). Il porte sur les déplacements inter-ponte des tortues olivâtres et des tortues luths de l'Est guyanais.

4.1 Contexte et hypothèses

L'aire de répartition de la tortue olivâtre s'étend à tous les océans tropicaux et subtropicaux (Godfrey & Godley, 2008). Cette espèce a été étudiée dans le Pacifique (Polovina *et al.*, 2004; Swimmer *et al.*, 2006; Plotkin, 2010), la mer d'Arafura au nord de l'Australie (Whiting *et al.*, 2007; McMahon *et al.*, 2007; Hamel *et al.*, 2008; Pikesley *et al.*, 2013), et dans les océans Indien (Rees *et al.*, 2012) et Atlantique (Reis *et al.*, 2010; Maxwell *et al.*, 2011; Plot *et al.*, 2015, 2012). Dans l'Atlantique équatorial, la Guyane française héberge l'un des principaux sites de ponte pour cette espèce (Kelle *et al.*, 2009). Étant donné le comportement actif de cette population durant la migration (Plot *et al.*, 2015) et l'inter-ponte (Plot *et al.*, 2012), et au regard de l'abondance de proies potentielles sur le plateau des Guyanes (Gueguen, 2000), nous faisons l'hypothèse que *les tortues olivâtres de Guyane française adoptent une stratégie de reproducteur sur revenu durant l'inter-ponte, en s'alimentant au cours de cette période*.

À l'exception de la Guyane française et de l'île Sainte-Croix dans les Caraïbes, les différentes études menées sur les déplacements de la tortue luth en inter-ponte ont mis en évidence une stratégie d'économie d'énergie durant cette période, *i.e.* des plongées longues, de dérive, ou de repos dans des eaux plus froides en profondeur (Eckert *et al.*, 1996; Reina *et al.*, 2005; Southwood *et al.*, 2005; Wallace *et al.*, 2005; Okuyama *et al.*, 2016). À l'inverse, dans les eaux de l'île Sainte-Croix dans les Caraïbes, l'analyse de sondes thermiques gastro-intestinales a montré l'évidence d'un comportement d'alimentation occasionnel (opportuniste) durant des plongées profondes (Casey *et al.*, 2010). De même, dans l'Ouest guyanais, plusieurs études suggèrent un comportement actif de cette espèce, parfois associé à de la prise alimentaire (Fossette *et al.*, 2007, 2009; Georges *et al.*, 2007; Fossette *et al.*, 2008b). Toutefois, une récente étude basée sur les données morphométriques de 35 femelles adultes a démontré une perte de poids moyenne (± SE) de 46,8 ± 2,6 kg en 71 jours d'inter-ponte, soit une perte de 11% de sa masse initiale (409,0 ± 8,9 kg, Plot *et al.* 2013). Sur les deux populations de tortues luths présentent en Guyane française, uniquement celle de l'Ouest, à Yalimapo, a fait l'objet de suivis télémétriques. Tout comme sa voisine de l'Ouest guyanais, on s'attend à ce que *la population de tortues luths de l'Est guyanais adopte un comportement actif durant l'inter-ponte en réalisant des déplacements extensifs*.

4.2 Méthodologie

Les résultats de ce quatrième chapitre sont issus du suivi satellitaire de tortues olivâtres ($n = 18$) et de tortues luths ($n = 11$) équipées depuis le site de Rémire-Montjoly dans l'Est guyanais :

- Huit tortues olivâtres équipées en 2013 de balises SPLASH10-F-238A ;
- Dix tortues olivâtres équipées en 2014 de balises CTD-Fluo-SRDL ;
- Une tortue luth équipée en 2014 d'une balise SPLASH10-F-296A ;
- Et dix tortues luths équipées en 2015 de balises 9000-SRDL.

Pour estimer la surface du domaine vital utilisé par chaque espèce durant l'inter-ponte, la méthode des densités de Kernel a été employée à partir des positions (Argos et GPS) médianes journalières. La méthodologie est détaillée dans l'Annexe B. Parmi les dix tortues olivâtres équipées en 2013, deux individus (131354 et 131355) sont partis en migration juste après la pose de la balise et ont donc été écartés des analyses (Annexe B, Tableau 1). En 2014, quatre individus (130765, 136775, 136776 et 136778) ont également été écartés des analyses en raison d'une durée de suivi insuffisante (3, 1, 8 et 14 j, respectivement). Concernant les tortues olivâtres, nous n'aborderons que les résultats issus des balises CTD-Fluo-SRDL qui ont fourni une résolution plus fine comparée aux balises SPLASH10-F (pour les résultats issus des huit balises SPLASH10-F, se référer à l'Annexe B). Parmi les 11 tortues luths équipées en 2015, trois individus ont été écartés des analyses en raison d'une durée de suivi insuffisante (149686, 149687 et 149689) - Annexe C.

4.3 Variabilité interspécifique de la dispersion

Tortues olivâtres

Les données des déplacements horizontaux des 14 tortues olivâtres sont résumées dans l'Annexe B. Les individus sont restés à proximité des côtes durant toute la durée du suivi (ne dépassant pas l'isobathe des 20 m, Figure 4.1a), ce qui correspond à des eaux moins profondes que celles observées dans des études précédentes (50 m, Whiting *et al.* 2007; Maxwell *et al.* 2011; Rees *et al.* 2012).

Tortues luths

Comparées aux tortues olivâtres, les tortues luths se sont davantage éloignées des côtes durant l'inter-ponte, allant jusqu'à l'isobathe des 150 m, mais restant majoritairement entre 0 et 20 m de fond (Figure 4.1b). Cette forte dispersion concorde avec une précédente étude réalisée sur la population de l'Ouest guyanais qui s'est éloignée en moyenne (± SD) à 90,4 ± 47,7 km des côtes durant cette période (Fossette *et al.*, 2007).

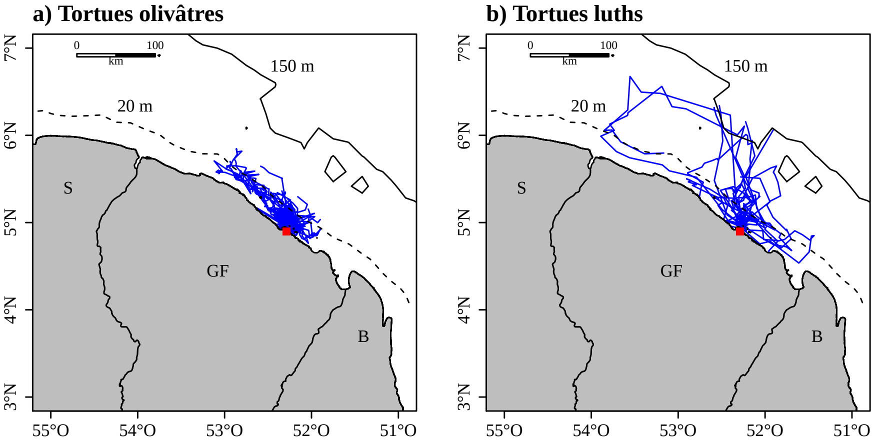


FIGURE 4.1 – Trajectoires des **(a)** 14 tortues olivâtres suivies en 2013 (*n* = 8) et 2014 (*n* = 6) et des **(b)** huit tortues luths suivies en 2014 (*n* = 1) et 2015 (*n* = 7). Ces deux espèces ont été suivies depuis le site de Rémire-Montjoly représenté par un carré rouge. GF correspond à Guyane française, S à Suriname et B à Brésil.

Ce patron de dispersion est également en accord avec la présence de méduses qui ont été identifiées sur le plateau continental guyanais (Fossette *et al.*, 2009) et qui semblent se concentrer dans des eaux turbides entre 10 et 20 m de profondeur. Cette étude suggère par conséquent un comportement de prospection alimentaire chez cette espèce durant l'interponte.

4.4 Fidélité au site de ponte

Tortues olivâtres

Chez les tortues olivâtres, la distance à la plage de ponte a varié au cours des semaines de suivi. Bien que les individus se soient davantage éloignés des côtes en 2013 par rapport à 2014 (jusqu'à 38 km *vs.* 20 km, Figure 4.2a), le même schéma de dispersion a été observé pour les deux années, à savoir une nette augmentation de la distance moyenne à la plage de ponte (± SE) durant les trois premières semaines (21,9 ± 0,6 km, min-max : 11,1-30,1 km). Entre la quatrième et la huitième semaine, les individus sont restés en moyenne (± SE) à 7,4 ± 0,2 km de leur plage de ponte (Figure 4.2a). La distance à la plage de ponte a toutefois varié d'un individu à l'autre, et ce, pour les deux années (test de Kruskal-Wallis : p < 0,001). En 2006 et 2007, le suivi satellitaire de cette même population de tortues olivâtres a montré des résultats similaires (Plot *et al.*, 2012), ce qui suggère une forte synchronisation chez cette espèce qui revient pondre après 28 jours en moyenne (Plot *et al.*, 2012). Ce phénomène appelé *arribadas*, a été mis en évidence chez différentes populations de tortues olivâtres (Eguchi *et al.*, 2007; Plot *et al.*, 2012), et est unique chez cette espèce, qui synchronise sa ponte avec ses congénères, très probablement pour saturer les prédateurs et donc augmenter le succès à l'éclosion.

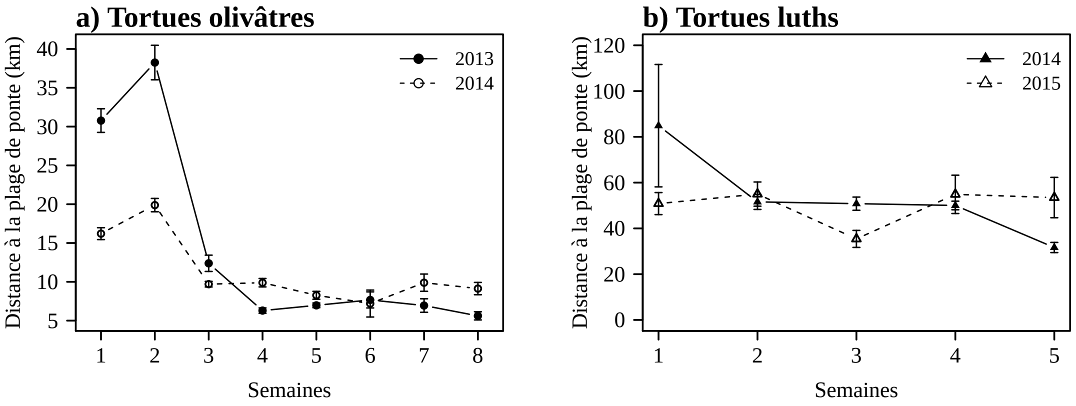


FIGURE 4.2 – Distances moyennes hebdomadaires (± SE) à la plage de ponte en fonction des semaines de suivi pour **(a)** les tortues olivâtres en 2013 (ronds pleins, $n = 8$) et 2014 (ronds vides, $n = 6$) et les **(b)** tortues luths suivies en 2014 (triangles pleins, $n = 1$) et 2015 (triangles vides, $n = 7$).

Tortues luths

Contrairement aux tortues olivâtres, les huit tortues luths étudiées sont restées en moyenne plus loin de leur plage de ponte, et ce, durant toute la durée du suivi (moyenne ± SE : 48,8 ± 1,4 km) - Figure 4.2b et Annexe C. La distance maximale au site de ponte a varié entre 59 et 241 km (moyenne ± SE : 153 km), ce qui coïncide avec le comportement d'autres populations de tortues luths de l'Atlantique (distance maximale de la plage de ponte au Gabon : 102 ± 50 km, Guyane française : 123 ± 51 km) et des Caraïbes (l'île de la Grenade : 134 ± 37 km) (Georges *et al.*, 2007), et pourrait être assimilé à de la prospection alimentaire.

4.5 Surface des domaines vitaux

Tortues olivâtres

Une faible différence interannuelle du centre d'activité (Kernel à 50%) a été observée chez la tortue olivâtre entre 2013 et 2014 (434 *vs.* 398 km², respectivement). La superficie du domaine vital (Kernel à 90%) a été quant à elle, deux fois plus grande en 2013 qu'en 2014 (3257 *vs.* 1587 km², respectivement). Les surfaces moyennes du domaine vital et du centre d'activité pour les deux années confondues se sont étendues sur 2916 km² et 423 km², respectivement (Figure 4.3a). À ce jour, il n'existe que deux études portant sur l'analyse du domaine vital de cette espèce. Menées en Afrique Centrale (Maxwell *et al.*, 2011) et au Brésil (Da Silva *et al.*, 2011), ces deux récentes études ont permis de délimiter un centre d'activité supérieur à celui de la Guyane française (Afrique : 4414 km², Brésil : 5223 km² vs. Guyane française : 1267 km²), ce qui renforce l'idée d'une forte fidélité au site de ponte observée chez la population de Guyane. Comme cela a été démontré chez d'autres espèces de tortues marines, ce domaine vital restreint suggère une stratégie pour économiser de l'énergie en limitant les déplacements durant l'inter-ponte (Stoneburner, 1982; Blanco *et al.*, 2013; Maxwell *et al.*, 2011; Esteban *et al.*, 2015), mais il pourrait aussi être lié à la distribution de leurs proies à proximité de la plage de ponte.

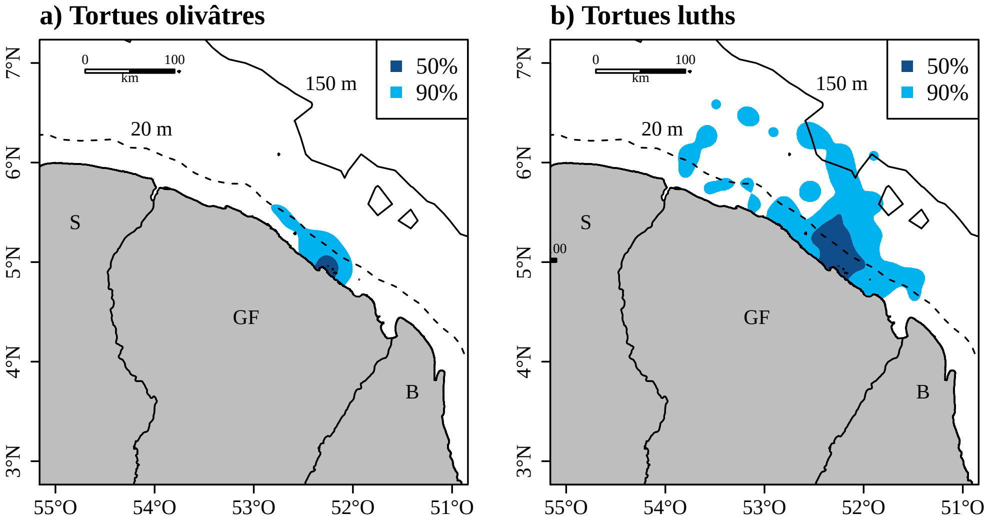


FIGURE 4.3 – (**a**) Contours issus des densités de Kernel (90% en turquoise et 50% en bleu foncé) des 14 tortues olivâtres suivies en 2013 et 2014 et (**b**) des huit tortues luths suivies en 2014 et 2015. GF correspond à Guyane française, S à Suriname et B à Brésil.

Tortues luths

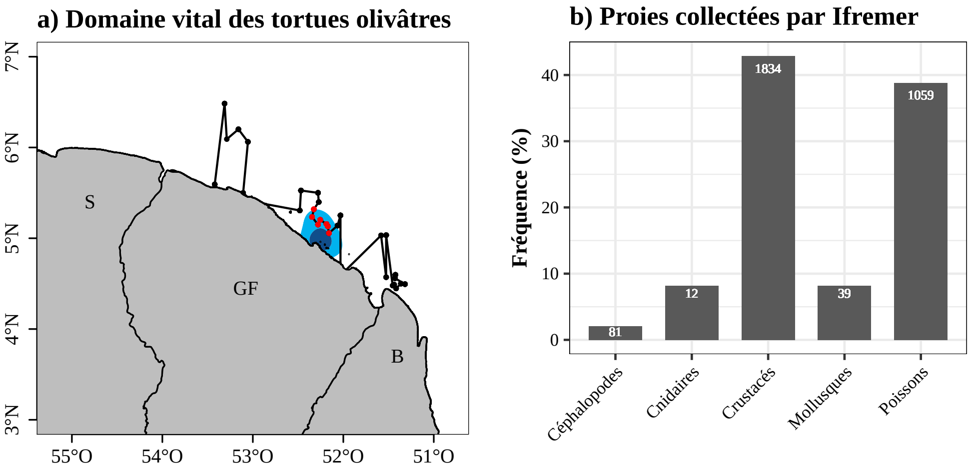
Chez la tortue luth, la surface du domaine vital total (Kernel à 90%) a été jusqu'à 5,6 fois plus importante que celle de la tortue olivâtre, couvrant une surface de 16439 km² (Figure 4.3b). En ce qui concerne la surface du centre d'activité (Kernel à 50%), elle a été jusqu'à six fois plus importante pour les tortues luths que pour les olivâtres (2725 *vs.* 423 km², respectivement). Un comportement similaire a été observé chez la tortue luth de l'Ouest guyanais, qui est restée majoritairement à l'embouchure du fleuve Maroni durant l'inter-ponte (Fossette *et al.*, 2007; Georges *et al.*, 2007). Cet important domaine vital a également été observé chez d'autres populations de tortues luths au Costa Rica (2092,2 km², Shillinger *et al.* 2010) ou encore en Floride, avec un habitat en inter-ponte s'étendant jusqu'à 60 km au large et 215 km le long de la côte américaine (Eckert *et al.*, 2006), probablement pour s'alimenter.

4.6 Disponibilité en proies potentielles et conditions océanographiques

Tortues olivâtres

Entre le 15 et 20/11/2014, 31 prélèvements de proies potentielles des tortues olivâtres ont été réalisés par l'Ifremer le long de la Guyane française, et à des profondeurs situées entre 12 et 51,8 m. Un total de 8730 organismes appartenant à cinq groupes différents a été collecté : crustacés (n = 4486), poissons (n = 3063), mollusques (n = 976), céphalopodes (n = 162) et cnidaires (n = 17).

Sur les 31 échantillons réalisés, le groupe d'épifaune le plus abondant a été les crustacés, correspondant à 51% des échantillons, suivi par le groupe des poissons (35%). Sept échantillons ont été collectés au sein du domaine vital des tortues olivâtres (contour à 90%) en 2014 (Figure 4.4a). Au sein de ce domaine vital, les deux groupes les plus abondants ont été les crustacés (43%, *e.g.* le crabe bleu) et les poissons (39%, *e.g.* l'acoupa, Figure 4.4a), deux groupes d'espèces benthiques faisant partie du régime alimentaire des tortues olivâtres (Lutz & Musick, 1996). Ces données permettent donc de confirmer la présence de proies potentielles sur l'aire de répartition des tortues olivâtres, une espèce carnivore qui pourrait ainsi s'alimenter durant l'inter-ponte, comme cela a été démontré au large de l'état de Sergipe au Brésil (Colman *et al.*, 2014).



a) Domaine vital des tortues olivâtres

b) Proies collectées par Ifremer

FIGURE 4.4 – (**a**) Transects (ligne noire) et prélèvements (points noirs) réalisés par l'Ifremer en Guyane française en 2014. Les points rouges correspondent aux échantillonnages réalisés dans le domaine vital des tortues olivâtres. (**b**) Pourcentages d'individus collectés par le chalut au sein du domaine vital (Kernel à 90%) en fonction des cinq groupes de proies identifiés. Les numéros blancs dans (**b**) correspondent à l'abondance des individus pour chaque groupe.

En 2014, les balises CTD-Fluo-SRDL des tortues olivâtres ont enregistré 91 températures variant entre 26,1 et 28,1 °C (moyenne ± SD : 26,7 ± 0,4 °C), et 84 valeurs de salinités, variant entre 19,9 et 36,4 psu (moyenne ± SD : 32,8 ± 5 psu) - Figure 4.5. En 2014, tous les individus ont donc traversé trois patchs de densité. Cette forte variabilité s'explique par la présence de nombreux fleuves à proximité du site de ponte (Jounneau & Pujos, 1988). Les tortues olivâtres se sont donc déplacées dans différents types de masses d'eau caractérisées par leur réflectance, *i.e.* des eaux dites 'vertes' (jusqu'à l'isobathe des 20 m) et des eaux 'beiges' situées à l'embouchure des fleuves (Froidefond *et al.*, 2002). Tout comme les tortues caouannes suivies au sud-ouest de la Floride (0-40 psu, Foley *et al.*, 2006) et la tortue de Kemp dans le Golfe du Mexique (4,5-36 psu, Metz, 2004), les résultats de notre étude suggèrent une forte tolérance à des conditions océanographiques contrastées, notamment en termes de salinité.

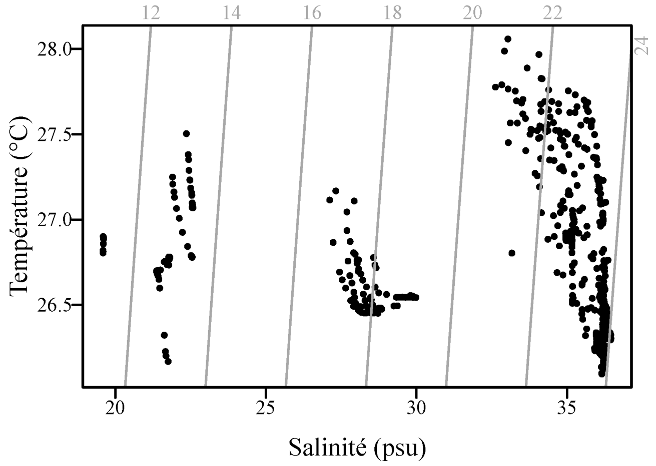


FIGURE 4.5 – Diagramme Température-Salinité issu des six balises CTD-Fluo-SRDL déployées sur les tortues olivâtres en 2014. Les lignes et les nombres en gris représentent les isopygnes et les valeurs de densité de l'eau.

4.7 Comportement de plongée

Tortues olivâtres

Sur l'ensemble de la période, la profondeur maximale moyenne de plongée (± SD) a été de 5,6 ± 4,4 m (min-max : 0-35 m), et 65% des plongées ont été réalisées dans les cinq premiers mètres (Figure 4.6a). On a observé une variabilité interindividuelle de la profondeur de plongée (test de Kruskal-Wallis : $p < 0{,}001$), mais aucune différence significative entre le jour et la nuit n'a été mise en évidence (moyenne ± SD : 6,2 ± 3,6 *vs.* 5,2 ± 4,7 m, test de Mann-Whitney : $p = 0{,}8438$).

La durée moyenne de plongée (± SD) a été de 8,6 ± 12,4 min et 77% des plongées ont duré moins de 10 min (Figure 4.6b). On a observé une variabilité interindividuelle de la durée de plongée (test de Kruskal-Wallis : p < 0,001), mais aucune différence significative entre le jour et la nuit n'a été identifiée (moyenne ± SD : 9,3 ± 9,7 *vs.* 8,2 ± 13,6 min, test de Mann-Whitney : p = 0,9905). Concernant la forme des plongées, 59% d'entre elles ont été en U (TAD > 0,75), et 37% en V (0,5 < TAD < 0,75). Enfin, 83% des plongées ont été réalisées sur le fond (benthiques), ce qui concorde avec la distribution de leurs proies, et tend à confirmer un comportement de prospection alimentaire au cours de l'inter-ponte.

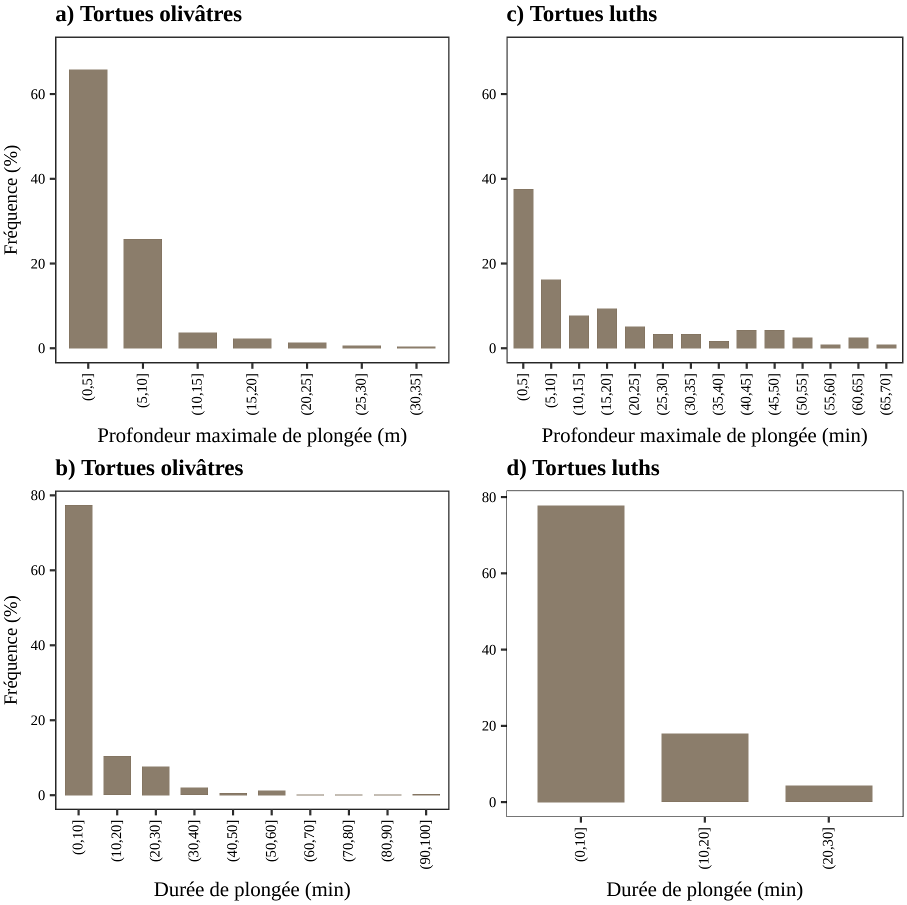


FIGURE 4.6 – Histogrammes des profondeurs maximales de plongée (**a** et **c**) et des durées de plongée (**b** et **d**) issues des huit tortues olivâtres suivies en 2014 et des sept tortues luths suivies en 2015.

Tortues luths

Les tortues luths de l'Est guyanais ont réalisé des plongées peu profondes (37% des plongées < 5 m, Figure 4.6c) et courtes (78% des plongées < 10 min, Figure 4.6d), ce qui est en accord avec les populations de l'est du Pacifique (Wallace *et al.*, 2005; Reina *et al.*, 2005) et de la Mer de Chine (Eckert *et al.*, 1996). Les tortues luths ont donc plongé bien en dessous de leur limite de plongée aérobique qui est estimée entre 33 et 67 min (Southwood *et al.*, 1999), limitant ainsi la dépense énergétique.

La profondeur maximale et la durée de plongée ont été significativement différentes d'un individu à l'autre (test de Kruskal-Wallis : p < 0,001), confirmant la forte plasticité comportementale déjà observée chez cette espèce (Fossette *et al.*, 2007), plasticité et qui pourrait être liée à des différences de condition corporelle ou de conditions océanographiques rencontrées. Les individus ont plongé plus profondément (moyenne ± SD : 20,1 ± 16,8 *vs.* 13,6 ± 17,2 m, test de Mann-Whitney : p < 0,05), et plus longtemps le jour que la nuit (moyenne ± SD : 7,7 ± 5,7 *vs.* 5,2 ± 5,8 min, test de Mann-Whitney : p < 0,05). Ces résultats concordent avec les travaux de Fossette *et al.* (2007), et tendent par conséquent à confirmer l'hypothèse que les tortues luths s'alimentent principalement la nuit (Eckert, 2002), lorsque le macrozooplancton gélatineux remonte en surface au cours des migrations nycthémérales.

Plus de la moitié des plongées (56%) étaient benthiques (*vs.* 44% pélagiques), ce qui confirme l'influence partielle de la bathymétrie sur le comportement de plongée des tortues luths (Fossette *et al.*, 2007; Okuyama *et al.*, 2016). Concernant la forme des plongées, 93% d'entre elles ont été en V (0,5 < TAD < 0,75), ce qui est commun chez cette espèce, et semble indiquer une activité de transit ou d'exploration (Hindell *et al.*, 1991; Schreer & Testa, 1996; Lesage *et al.*, 1999), induisant une dépense énergétique plus élevée (Reina *et al.*, 2005).

4.8 Évolution temporelle du comportement de plongée

Tortues olivâtres

Nous avons pu mettre en évidence des variations du comportement de plongée au cours de l'inter-ponte chez les tortues olivâtres. En effet, les individus ont réalisé des plongées plus longues et plus profondes durant les trois premières semaines de suivi (moyenne ± SE : 29,7 ± 0,4 min et 12,6 ± 0,1 m), puis des plongées plus courtes et plus en surface sur le reste de la période (moyenne ± SE : 25,9 ± 0,3 min et 10,4 ± 0,09 m) - Figures 4.7a et b. Ces résultats concordent avec de précédentes études réalisées sur cette espèce dans la mer d'Oman (Rees *et al.*, 2012) et en Guyane française (Plot, 2012). Ils renforcent l'idée d'une synchronisation interindividuelle de la ponte chez cette espèce.

Tortues luths

À l'inverse, les tortues luths de l'Est guyanais ont réalisé des plongées de plus en plus profondes et de plus en plus longues au fur et à mesure des semaines (Figures 4.7c et d). Ce résultat pourrait indiquer un ajustement du comportement en vue de la migration post-ponte. Les tortues luths pourraient ainsi augmenter leurs capacités de plongée au cours de la saison d'inter-ponte (entre 53,6 et 81,8 m, Fossette *et al.* 2010c). Il a également été suggéré que les prédateurs plongeurs réalisent des plongées plus longues dans des zones où le succès de pêche est plus élevé (Thompson & Fedak, 2001), ce qui concorderait avec l'hypothèse d'un comportement d'alimentation chez la tortue luth de l'est guyanais durant la saison d'inter-ponte.

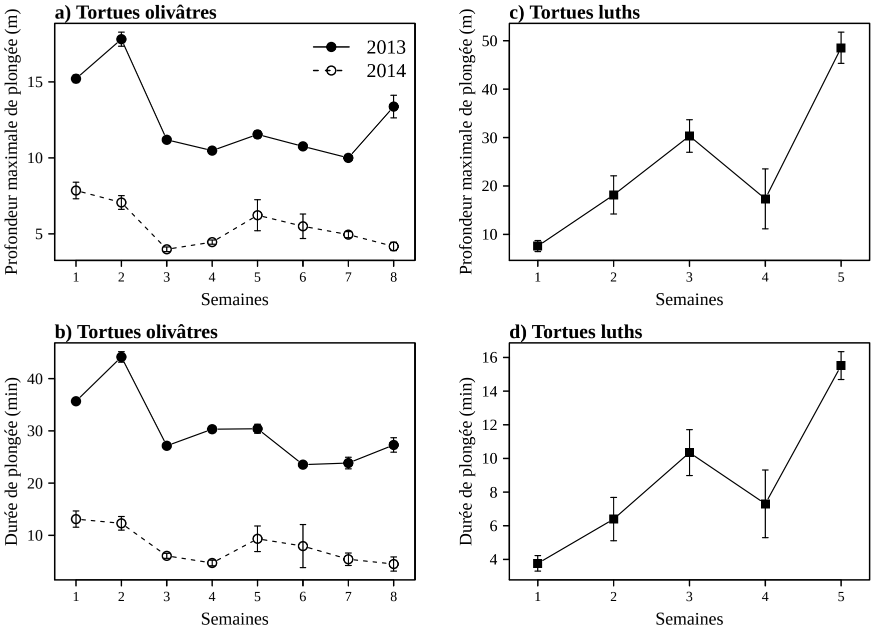


FIGURE 4.7 – Moyennes (± SE) des profondeurs maximales de plongée (**a** et **c**) et des durées de plongée (**b** et **d**) issues des 14 tortues olivâtres suivies en 2013 et 2014 et des six tortues luths suivies en 2015.

4.9 Résumé

Le suivi des populations de tortues olivâtres et de tortues luths de l'Est guyanais a permis de fournir des informations capitales sur (1) la surface du domaine vital occupé, (2) les caractéristiques de l'habitat ainsi que sur (3) les différentes activités réalisées durant cette période coûteuse en énergie qu'est l'inter-ponte. Il s'agit également de la première étude réalisée sur la population de tortues luths de l'Est guyanais, qui, bien que génétiquement différente de celle de l'Ouest (Molfetti *et al.*, 2013), adopte un comportement similaire. Mes principaux résultats peuvent ainsi être résumés par :

- L'existence d'un domaine vital plus important chez la tortue luth (2552 km²) que chez l'olivâtre (423 km²).
- La présence de proies potentielles de la tortue olivâtre (crustacés et poissons).
- Durant la première moitié de l'inter-ponte chez l'olivâtre : l'éloignement de la plage de ponte (moyenne ± SD : 21,9 ± 24,7 km), des plongées plus profondes (12,6 ± 7,4 m) et plus longues (29,7 ± 21,0 min), qui témoignent d'une synchronisation interindividuelle lors de la ponte.

- L'utilisation d'un habitat estuarien, variable en terme de salinité (32,8 ± 5 psu).
- Chez la tortue luth, des plongées majoritairement de transit (en V), plus courtes et plus en surface la nuit, en lien avec les migrations nycthémérales.

Après la saison d'inter-ponte, les tortues luths entament leur migration océanique (Chapitre 6), tandis que les tortues olivâtres et les tortues vertes adoptent un schéma migratoire côtier (Chapitre 5).

CHAPITRE 5

Déplacements post-ponte : la migration côtière des tortues vertes et olivâtres

Sommaire

Ce cinquième chapitre concerne la synthèse de trois articles publiés dans *Biological Conservation* (Annexe D), *PLoS ONE* (Annexe E) et *Progress in Oceanography* (Annexe F), et porte sur la migration côtière des tortues vertes et tortues olivâtres au départ de la Guyane française (sites d'Awala-Yalimapo et de Rémire-Montjoly).

5.1 Contexte et hypothèses

Dans l'Atlantique équatorial de l'ouest, les habitats d'alimentation utilisés par la tortue verte ont été identifiés dans les années 1970 à l'aide de la méthode de CMR. Plusieurs individus bagués en Guyane française ont ensuite été observés le long des états du Ceará et Paraíba au Brésil (Pritchard, 1976), ce qui suggère une migration vers le sud-est depuis la Guyane. À l'âge adulte, la tortue verte est strictement herbivore, se nourrissant principalement d'herbiers et de macroalgues, dont la croissance dépend de conditions particulières en termes de lumière, de température et de nutriments (Lee & Dunton, 1997). Or, chaque année, le fleuve Amazone déverse près de 115.10^7 tonnes de sédiments dans l'Atlantique, rendant la côte nord-est de l'Amérique latine, dont la Guyane française, défavorable à la prolifération d'herbiers marins (Milliman & Meade, 1983; DeMaster *et al.*, 1996). Si les tortues vertes de Guyane française migrent bel et bien en direction du Brésil, on s'attend à ce qu'elles *ajustent leur comportement en fonction du courant nord-brésilien et du panache amazonien, tout en ciblant des eaux claies riches en herbiers pour s'alimenter.*

Une précédente étude portant sur le suivi satellitaire de la population de tortues olivâtres de Guyane française a mis en évidence une migration côtière avec des individus qui utilisent majoritairement le plateau continental. Or, ce plateau continental est une zone productive, façonnée par de puissants tourbillons anticycloniques (Didden & Schott, 1993) et une thermocline marquée agrégeant des proies (Hakoyama *et al.*, 1994). À ce jour, aucune étude n'a relié son comportement de prospection alimentaire aux structures océanographiques, aussi bien dans la dimension horizontale que verticale. Cette espèce étant carnivore et généraliste (Colman *et al.*, 2014; Bjorndal, 1985; McMahon *et al.*, 2007), on s'attend à ce qu'elle *utilise ces structures océanographiques particulières au cours de la migration pour s'alimenter.*

5.2 Méthodologie

Les résultats de ce cinquième chapitre sont issus du suivi satellitaire de 46 femelles adultes suivies depuis la plage d'Awala-Yalimapo (tortues vertes, $n = 18$), la Réserve Naturelle de Galibi au Suriname (tortues vertes, $n = 8$) et la plage de Rémire-Montjoly (tortues olivâtres, $n = 20$) :

- Seize tortues vertes équipées en 2012 de balises SPLASH10-F-238A ;
- Dix tortues vertes équipées en 2014 de balises CTD-Fluo-SRDL ;

- Huit tortues olivâtres équipées en 2013 de balises SPLASH10-F-296A ;
- Deux tortues olivâtres équipées en 2013 de balises CTD-Fluo-SRDL ;
- Et de dix tortues olivâtres équipées en 2014 de balises CTD-Fluo-SRDL.

Le comportement d'alimentation a tout d'abord été identifié à l'aide des méthodes du *First Passage Time* pour les tortues vertes et du *Residence Time* pour les tortues olivâtres. Parmi les 26 tortues vertes équipées entre 2012 et 2014, sept individus ont dû être écartés des analyses en raison du nombre insuffisant de données collectées. De plus, en raison du nombre insuffisant de données de plongées collectées par les balises CTD-Fluo-SRDL déployées sur les tortues vertes, seules les données issues des balises SPLASH10-F ont été utilisées pour l'analyse du comportement de plongée de cette espèce. Afin d'évaluer l'influence du panache amazonien sur le déplacement des tortues vertes en migration, les trajectoires de ces individus ont été découpées en trois phases, *i.e.* avant le panache (P1), dans le panache (P2) et après le panache (P3). Les trajectoires des tortues vertes ont été segmentées en trois phases à l'aide du coefficient d'atténuation de la lumière (k_d exprimé en m^{-1}), variable extraite depuis la base de données *oceancolour* (satellite MODIS Aqua). Pour évaluer l'influence des courants océaniques sur les déplacements des deux espèces, les données de courants ont été extraites depuis *Copernicus*. La méthodologie est détaillée dans l'Annexe E.

Sur les 20 tortues olivâtres équipées en 2013 et 2014, deux balises n'ont pas transmis de données. Cette espèce étant carnivore, la caractérisation de son habitat d'alimentation dans la dimension horizontale a été réalisée à partir de différentes variables telles que la biomasse de micronecton fournit par le modèle SEAPODYM, les données de courants de surface, de SST et de SSH fournies par *Copernicus*. Dans la dimension verticale, la méthode du *Hunting time* développée par Heerah *et al.* (2015) a ensuite été employée pour relier le comportement de chasse de cette espèce aux structures verticales de la colonne d'eau (*e.g.* thermocline, couche euphotique). Pour le comportement de plongée, seuls les résultats issus des balises CTD-Fluo-SRDL sont présentés dans ce chapitre, puisque ces balises ont fourni une meilleure résolution comparée aux balises SPLASH10-F (pour les résultats issus des SPLASH10-F se référer à l'Annexe F). La méthodologie est détaillée dans l'Annexe F.

5.3 Utilisation du plateau continental

Tortues vertes

Les 19 tortues vertes suivies ont toutes migré vers le sud-est, et ce, quelle que soit l'année de déploiement des balises (Annexes D et E) - Figures 5.1a et 5.2. À la différence des tortues vertes de Tortuguero qui migrent sur des distances bien plus faibles (moyenne : 512 km, Troëng *et al.* 2005) pour s'alimenter sur des herbiers situés proches de leur site de ponte, les tortues vertes de Guyane française ont réalisé une longue migration, parcourant en moyenne (± SD) 3450 ± 701 km (Annexe E). Un individu a notamment réalisé la plus longue migration post-ponte jamais enregistrée chez cette espèce à l'âge adulte, parcourant 5153 km. Tous les individus ont réalisé une migration côtière le long du plateau continental (< à l'isobathe des 100 m). Un comportement similaire a été mis en évidence dans le Pacifique le long de la côte mexicaine (Hart *et al.*, 2015). Bien que d'importantes distances aient déjà été documentées chez certaines populations de tortues vertes qui pondent sur des îles océaniques et traversent l'océan pour rejoindre leurs zones d'alimentation (Seminoff *et al.*, 2008; Godley *et al.*, 2001; Hays *et al.*, 1999), aucune migration côtière sur d'aussi longues distances n'avait encore été mise en évidence dans l'Atlantique occidental. À l'exception d'une tortue qui s'est arrêtée au large de Cayenne en 2012 (en Phase P1), toutes les autres ont décrit un comportement de prospection alimentaire le long des états de Ceará et Paraíba au Brésil (Figures 5.1a et 5.2).

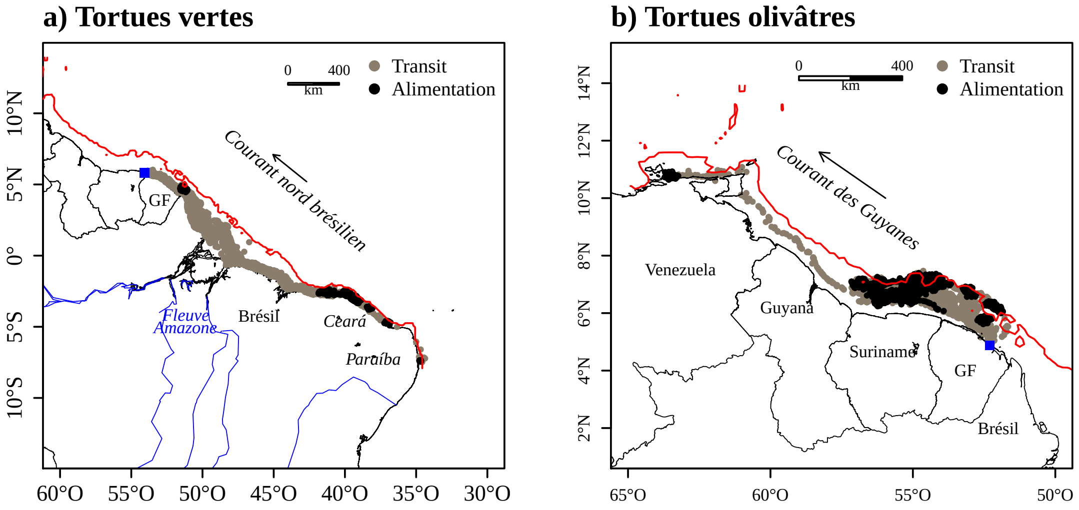


FIGURE 5.1 – Trajectoires post-ponte des 19 tortues vertes suivies en 2012 et 2014 (**a**) et des 18 tortues olivâtres suivies en 2013 et 2014 (**b**) en Guyane française. Les lignes rouges délimitent l'isobathe des 100 m. Le carré bleu correspond au point de départ en Guyane française.

Dans les années 1970, plusieurs tortues vertes provenant de la Guyane française ont été observées (Pritchard, 1976) en train de s'alimenter sur la zone d'alimentation de l'état de Ceará au Brésil. À la différence des tortues vertes de Tortuguero qui utilisent différentes zones d'alimentation, les tortues vertes de Guyane française décrivent une surprenante synchronisation, en utilisant des aires d'alimentation communes situées à la fin de leur trajet migratoire. Pour compenser cette migration coûteuse en énergie, les tortues vertes ont réalisé plusieurs haltes migratoires avant d'atteindre leurs aires d'alimentation au Brésil (Figure 5.2). Ces haltes migratoires sont très probablement utilisées pour se reposer ou s'alimenter en route, comme cela a déjà été observé chez cette espèce en Méditerranée

FIGURE 5.2 – Trajectoires post-ponte et haltes migratoires (étoiles) des 16 tortues vertes suivies en 2012. La taille des étoiles est proportionnelle au nombre d'individus ayant utilisé ces haltes migratoires pendant plus de cinq jours (dans l'ordre : 7, 7, 5, 2, 4 et 3).

(Godley *et al.*, 2002) ou encore dans le Pacifique (Cheng, 2000).

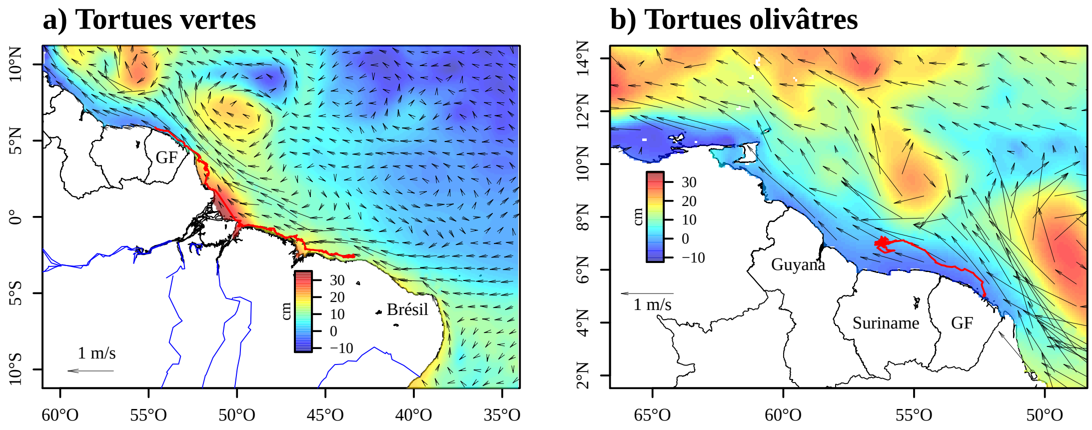
Tortues olivâtres

Les 18 tortues olivâtres ont parcouru de plus faibles distances que les tortues vertes (moyenne ± SD : 1502 ± 689 km, Annexe F), restant également sur le plateau continental (< à l'isobathe des 100 m). Ce résultat diffère de l'étude de Plot *et al.* (2015) qui avait observé une plasticité comportementale dans la dispersion puisque les individus avaient utilisés deux autres habitats durant leur migration, *i.e.* la pente continentale et les eaux profondes. En revanche, tous les individus ont migré sur de courtes distances pour rejoindre leurs zones d'alimentation (moyenne ± SD : 366,8 ± 294,5 km), ce qui est en accord avec les résultats de précédentes études menées sur cette espèce (Whiting *et al.*, 2007; Rees *et al.*, 2012; Plot *et al.*, 2015). Cette courte migration est probablement liée à la durée de l'intervalle de migration, qui est relativement courte chez cette espèce en Guyane, comparée aux autres tortues marines, *i.e.* 1-2 ans (ONCFS). Bien que cantonnées au plateau continental, les tortues olivâtres ont migré dans la direction opposée à celle des tortues vertes, à savoir vers le nord-ouest (Figure 5.1b). À l'exception d'une tortue qui a réalisé une longue migration jusqu'aux côtes vénézuéliennes, les 17 autres sont restées dans les eaux de la Guyane française et du Suriname, restant par conséquent relativement proches de leur site de ponte.

5.4 Influence des courants océaniques

Tortues vertes

Sur l'intégralité des positions disponibles, 88% ont été associées à un fort courant se dirigeant vers le nord-ouest, *i.e.* le courant nord-brésilien (Figure 5.3a). Les tortues vertes ont donc migré à contre-courant durant l'intégralité de leur trajet. Toutefois, les zones de plus fortes intensités (jusqu'à > 1 m.s^{-1}) ont été situées parallèlement aux côtes et à environ 100 km au large. Or, les individus sont restés cantonnés aux côtes (moyenne ± SD : 22 ± 24,4 km) durant toute la durée du suivi, expérimentant donc des courants de plus faible intensité. Pour compenser l'effet du courant, les individus ont tous migré relativement rapidement, à une vitesse de nage moyenne (± SD, corrigée des courants) de 0,84 ± 0,55 m.s^{-1} (~3 ± 1,9 km.h^{-1}). En effet, le débit du courant nord-brésilien est très puissant et peut atteindre 36 Sv (1 Sv = $10^6 m^3 s^{-1}$, Johns *et al.* 1998). En se rapprochant de la côte, ce courant est atténué en raison de la diminution de la bathymétrie et de l'augmentation des forces de frottement (Feddersen *et al.*, 2003; Hansen *et al.*, 2014), ce qui pourrait expliquer la proximité des déplacements de tortues le long de la côte pour économiser de l'énergie durant la migration. En quittant la Guyane française en avril, les individus éviteraient également le débit maximal du courant nord-brésilien (pic en juillet-août, Johns *et al.* 1998).



a) Tortues vertes

b) Tortues olivâtres

FIGURE 5.3 – Cartes hebdomadaires des courants océaniques (direction et vitesse en m.s^{-1}, extraits de Copernicus) et de la hauteur d'eau (code couleur, en cm, extraite de Copernicus) pour la période du 16-22/04/2012 pour les tortues vertes suivies en 2012 (**a**) et du 16-18/08/2013 pour les tortues olivâtres suivies en 2013 (**b**). Les trajectoires des individus (**a**) 115445 et (**b**) 131354 ont été superposées. Pour une meilleure visualisation, la résolution spatiale des données de courants a été fixée à 0,8 degré décimal.

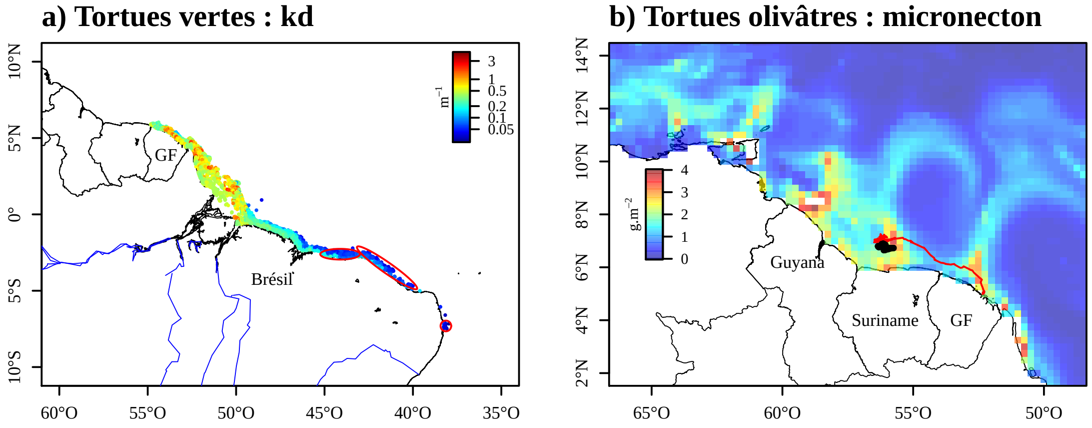
Tortues olivâtres

À l'inverse des tortues vertes qui ont migré à contre-courant, les tortues olivâtres ont migré dans le sens du courant tout en évitant les tourbillons anticycloniques qui sont associés au puissant courant des Guyanes (jusqu'à > 1,5 m.s^{-1}, Didden & Schott 1993; Lumpkin & Garzoli 2005) et à des SSH élevées (Figure 5.3b). Cette hypothèse semble confirmée par l'étude de Plot *et al.* (2015) réalisée sur la même population en 2006, et pour laquelle un seul individu avait été entraîné par ces puissants tourbillons. Les positions des individus ont donc été associées à des SSH et des courants plus faibles qu'au large (2,9 ± 3,8 cm et 0,53 ± 0,22 m.s^{-1}). Les tortues olivâtres semblent par conséquent cibler des zones peu turbulentes situées à proximité de la côte, et probablement riches en nourriture.

5.5 Influence du panache amazonien

Tortues vertes

Globalement, une augmentation de la distance à la côte a été observée durant la traversée du panache amazonien (Figure 5.1a). La distance séparant les individus de la côte a été jusqu'à deux fois plus élevée durant de la phase P2 (moyenne ± SD : 46,6 ± 45,7 km), comparée aux phases P1 (avant le panache : 13,5 ± 8,4 km) et P3 (après le panache : 17,3 ± 11,3 km). Les individus pourraient traverser plus au large pour éviter les eaux turbides et turbulentes du panache, ou bien pour réduire la distance parcourue en choisissant le trajet le plus court pour rejoindre les zones d'alimentation le plus rapidement possible (Godley *et al.*, 2002).



a) Tortues vertes : kd

b) Tortues olivâtres : micronecton

FIGURE 5.4 – (**a**) Distribution du coefficient d'atténuation de la lumière (k$_d$, en m^{-1}, depuis *oceancolour*) extrait le long des trajectoires des 21 tortues vertes suivies en 2012 et 2014. Dans (**a**), le k$_d$ a été log transformé pour une meilleure visualisation et les ellipses rouges désignent les zones d'alimentation identifiées. (**b**) Carte hebdomadaire de la biomasse de micronecton (en g.m^{-2}, extraite de SEAPODYM) sur la période du 16-18/08/2013 pour les tortues olivâtres suivies en 2013. La trajectoire de l'individu 131354 a été superposée dans (**b**) et les points noirs correspondent aux positions de cet individu pour la semaine considérée.

La distance séparant le site de ponte de la première zone d'alimentation a diminué avec l'augmentation du temps passé dans le panache (coefficient : -4,9891, $p < 0,01$). Ce résultat suggère que la traversée de cette zone turbulente engendre une perte énergétique importante puisqu'à l'inverse, les individus qui ont passé moins de temps dans le panache sont allés s'alimenter plus loin de leur site de ponte (plus au sud). La date du départ en migration est également un paramètre important puisque les premiers individus à quitter le site de ponte en avril ont probablement évité la période au cours de laquelle le débit du panache est maximal (mai-juin, Nikiema *et al.*, 2007).

Les aires d'alimentation des tortues vertes ont été caractérisées par des eaux claires et peu turbides, rassemblant ainsi les conditions favorables à la prolifération d'herbiers et d'algues marines (Lee *et al.*, 2010), les deux principales sources de nourriture de cette espèce herbivore à l'âge adulte (Lutz & Musick, 1996). Ces habitats d'alimentation contrastent en effet avec ceux situés à l'embouchure de l'Amazone (Figure 5.4a). Les grandes quantités de sédiments et de particules en suspension charriées par le fleuve Amazone dans l'Atlantique rendent les eaux très turbides à sa périphérie (Milliman & Meade, 1983; DeMaster *et al.*, 1996; Molleri *et al.*, 2010), obligeant ainsi les tortues vertes à migrer vers l'est, bien au-delà du panache amazonien pour accéder aux herbiers.

Tortues olivâtres

Les tortues olivâtres ont également subi l'influence du panache amazonien, qui se déverse en continu dans l'Atlantique et enrichit le plateau continental en nutriments. Le panache amazonien rend donc le domaine néritique très productif et riche en micronecton (proies potentielles) pour les tortues olivâtres (Figure 5.4b). D'après les cartes de micronecton, les tourbillons anticycloniques ont été pauvres en biomasse en leur cœur mais riches en micronecton en leur périphérie, zone utilisée par les tortues olivâtres en alimentation. Les nutriments en provenance du fleuve Amazone s'agrègent donc ensuite en périphérie de ces tourbillons (Froidefond *et al.*, 2002; Baklouti *et al.*, 2007), rendant le plateau continental riche en organismes, du phytoplancton au micronecton (proies potentielles pour cette espèce carnivore), comme cela a déjà été démontré dans le canal du Mozambique (Sabarros *et al.*, 2009).

5.6 Comportement de plongée

Tortues vertes

La profondeur moyenne atteinte a été de 32,0 ± 20,9 m (moyenne ± SD) et 71% des plongées ont été réalisées entre 10 et 30 m (Figure 5.5a). Les individus ont plongé légèrement plus profondément durant le transit (moyenne ± SD : 33,7 ± 25,1 *vs.* 29,5 ± 10,0 m, respectivement, test de Wilcoxon : $p < 0{,}001$), restant toutefois à de faibles profondeurs où suffisamment de lumière pénètre dans la colonne d'eau pour permettre le développement d'herbiers (Lee & Dunton, 1997; Lee *et al.*, 2007). D'après l'Université Fédérale de Rio Grande (FURG), plus de 30 000 ha d'herbiers marins recouvrent le plateau continental brésilien (0-25 °S, Copertino 2013).

La durée moyenne des plongées (± SD) a été de 35,1 ± 21,9 min (Figure 5.5b). La durée de plongée a varié significativement entre les individus (test de Kruskal-Wallis : p < 0,001), et 35% d'entre elles ont duré entre 30 et 40 min. De même, la durée de plongée est apparue légèrement plus courte durant le transit (moyenne ± SD : 33,6 ± 23,5 *vs.* 37,1 ± 19,1 m, respectivement, test de Wilcoxon : p < 0,001), et pourrait suggérer des coûts énergétiques élevés associés à la traversée du panache, incitant par conséquent les individus à remonter plus régulièrement à la surface pour respirer. Tout comme cela a été démontré chez les tortues caouannes qui utilisent des signaux odorants circulant dans l'air pour s'orienter (Endres & Lohmann, 2013), les tortues vertes de Guyane française pourraient adopter la même stratégie pour maintenir leur cap dans les eaux turbides de l'Amazone.

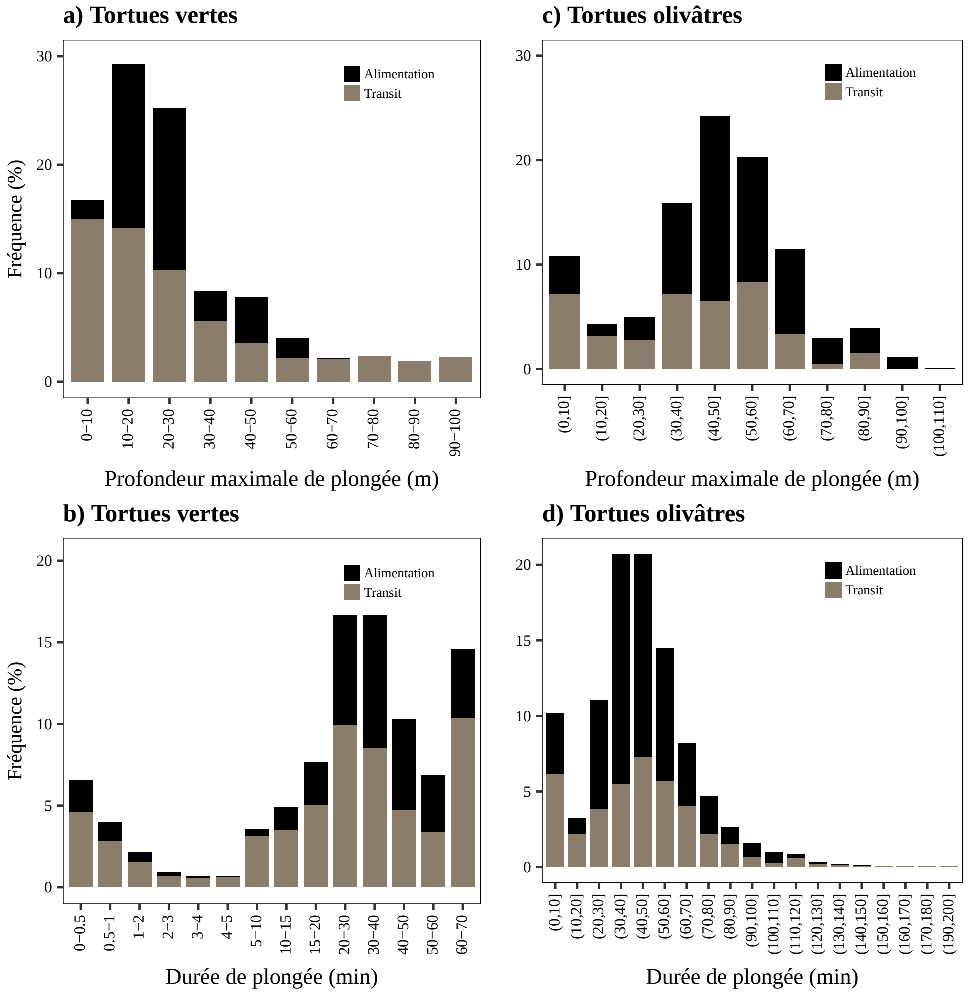


FIGURE 5.5 – Histogrammes des profondeurs maximales de plongée (**a** et **c**) et des durées de plongée (**b** et **d**) issues des 14 tortues vertes suivies en 2012 et des 10 tortues olivâtres suivies en 2014 pour les deux modes, *i.e.* transit en gris et alimentation en noir.

Tortues olivâtres

La profondeur moyenne enregistrée (± SD) par les balises CTD-Fluo-SRDL a été de 43,6 ± 20,6 m, et 72% des plongées ont été réalisées entre 30 et 70 m (Figure 5.5c).

Aucune différence significative concernant la profondeur de plongée entre le transit et l'alimentation n'a été observée (moyenne ± SD : 37,7 ± 21,8 *vs.* 47,6 ± 18,8 m, respectivement, test de Wilcoxon : p = 0,1055).

Les plongées ont duré en moyenne (± SD) 45,9 ± 24,5 min (min-max : 0,5-200 min), et 40% des plongées ont duré entre 30 et 50 min (Figure 5.5d). Aucune différence significative n'a été observée entre le transit et l'alimentation (moyenne ± SD : 46,0 ± 29,0 *vs.* 45,8 ± 21,1 min, respectivement, test de Wilcoxon : p = 0,1602).

Sur les 2817 profils de plongée enregistrés, 44% ont été benthiques et 56% pélagiques (bathymétrie-profondeur maximale > 3 m), et 70% des individus ont réalisé principalement des plongées pélagiques. Le TAD moyen a été de 0,8 ± 0,1, indiquant principalement des plongées en U, ce qui concorde avec les résultats de précédentes études sur cette espèce (McMahon *et al.*, 2007; Hamel *et al.*, 2008; Plot *et al.*, 2015), et confirme le comportement de prospection alimentaire ou de repos réalisé au fond ou dans la colonne d'eau.

5.7 Influence des structures verticales de la colonne d'eau

Tortues vertes

Les tortues vertes ont modifié leur comportement de plongée sous l'influence du panache amazonien. La profondeur maximale de plongée a été significativement différente selon la phase de la migration (test de Tukey USD : p < 0,001), étant plus profonde dans le panache et moins profonde avant le panache (moyenne ± SD : 38,7 ± 28,8 *vs.* 26,6 ± 25,3 m, respectivement) - Figure 5.6a. L'épaisseur du panache amazonien pouvant atteindre 10 m (Hu *et al.*, 2004), les tortues vertes pourraient plonger plus profondément durant la traversée pour éviter les eaux turbides et turbulentes de surface.

Tortues olivâtres

Les 1196 profils CTD ont enregistré 21775 données de températures et de salinité. La salinité a varié entre 7,3 et 36,3 psu et la température entre 21,5 et 30,0 °C, et tous les individus ont utilisé une large gamme de conditions océanographiques (Annexe F, Figure 6A). La profondeur de la thermocline (identifiée à partir du gradient de température issu des profils CTD) a varié entre 26,3 ± 2,3 m et 53,6 ± 9,4 m, pour une profondeur moyenne (± SD) de 43,4 ± 12,3 m (Annexe F, Figure 6B). Les tortues olivâtres ont passé en moyenne (± SD) 36,4 ± 21,6 min à chasser par plongée, soit 77 ± 18,3% de la durée totale des plongées (Annexe F, Tableau 2). Durant sa migration post-ponte, cette espèce semble donc chasser quasi continuellement, ce qui suggère un comportement opportuniste qui coïncide avec son régime alimentaire généraliste (Bjorndal, 1985; McMahon *et al.*, 2007).

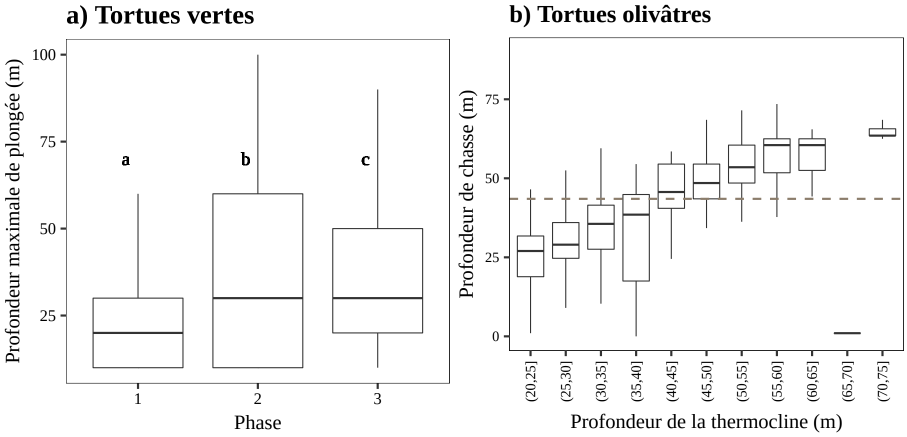


FIGURE 5.6 – (**a**) Boîtes à moustaches de la profondeur maximale de plongée des 14 tortues vertes suivies en 2012 en fonction de la phase de migration (1 : avant le panache, 2 : dans le panache et 3 : après le panache). Dans (**a**), les différentes lettres au-dessus des boîtes à moustaches indiquent que les trois groupes sont statistiquement différents. (**b**) Boîtes à moustaches de la profondeur de chasse en fonction de la profondeur de la thermocline des 10 tortues olivâtres suivies en 2014. La ligne en pointillés grise dans (**b**) correspond à la profondeur moyenne de chasse identifiée à l'aide de la méthode du *Hunting time* (issue de Heerah *et al.* 2015).

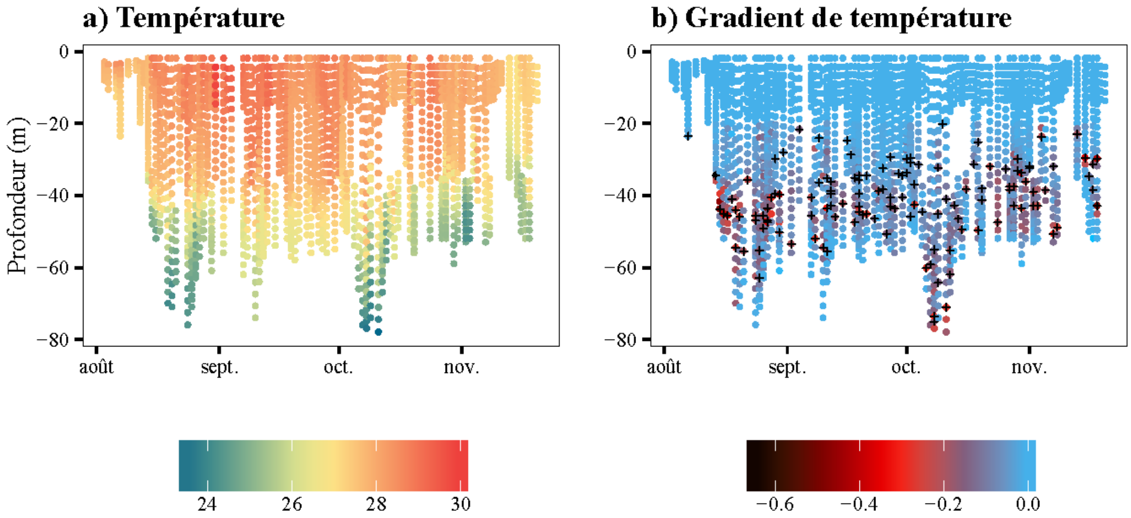


FIGURE 5.7 – (**a**) Profil de température (°C) de l'individu 135454 au cours du temps et (**b**) profil du gradient de température (°C.m^{-1}) pour ce même individu. Les croix noires dans (**b**) correspondent aux profondeurs moyennes de chasse identifiées à l'aide du *Hunting time*.

Les individus ont chassé en moyenne (± SD) à 43,5 ± 18,5 m. (Benoit-Bird *et al.*, 2013). La profondeur moyenne de chasse a augmenté proportionnellement et de manière significative avec la profondeur de la thermocline ($p < 0,001$, Figure 5.6b, Figure 5.7b), ce qui indique que les tortues olivâtres ciblent cette zone de fort gradient thermique lorsqu'elles s'alimentent. La thermocline joue en effet un rôle crucial dans la distribution verticale des organismes pélagiques (Hakoyama *et al.*, 1994), ce qui va par conséquent affecter la comportement de prospection alimentaire des prédateurs. Des comportements similaires ont déjà été observés chez les oiseaux et mammifères marins (Ballance *et al.*, 2001; Charrassin & Bost, 2001). Des analyses de contenus stomacaux réalisées sur des tortues olivâtres capturées à Hawaï indiquent que cette espèce peut aussi consommer des organismes pélagiques distribués en subsurface, *i.e.* pyrosomes et salpes (données non publiées, Laboratoire d'Honolulu, NMFS).

5.8 Résumé

Le suivi satellitaire de ces deux populations de tortues vertes et tortues olivâtres de Guyane française a permis de mettre en évidence des patrons migratoires différents et l'utilisation d'habitats distincts durant la migration post-ponte. Les principaux résultats peuvent être résumés comme suit :

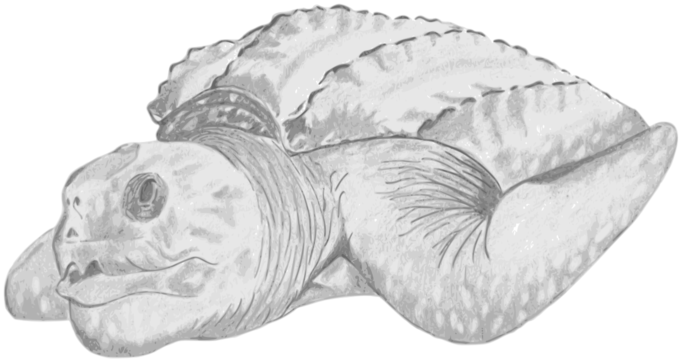
- Les tortues vertes et les tortues olivâtres ont réalisé une migration côtière sur le plateau continental.
- Les tortues vertes ont migré à contre-courant (vers le sud-est) tandis que les tortues olivâtres se sont dirigées vers le nord-ouest, dans le sens du courant des Guyanes.
- Les tortues vertes ont ciblé des zones d'alimentation au large des états de Ceará et Paraíba au Brésil et caractérisées par des eaux claires et riches en herbiers.
- Les tortues olivâtres ont ciblé les eaux productives et riches en micronecton localisées à la périphérie des tourbillons anticycloniques du plateau des Guyanes.
- Les tortues vertes ont ajusté leur comportement (distance à la côte et paramètres de plongée) au puissant courant nord-brésilien ainsi qu'au panache amazonien.
- Les tortues olivâtres ont chassé quasi continuellement en ciblant la profondeur de la thermocline.

À la différence des tortues vertes et des tortues olivâtres qui présentent des schémas migratoires essentiellement côtiers, les tortues luths vont réaliser une migration post-ponte océanique, que nous aborderons dans le chapitre suivant (Chapitre 6).

CHAPITRE 6

Déplacements post-ponte : la migration océanique des tortues luths

Sommaire



Ce sixième chapitre concerne la synthèse d'un article publié dans *Deep-Sea Research Part 1* (Annexe G), et qui porte sur la migration océanique des tortues luths de l'Est guyanais (site de Rémire-Montjoly).

6.1 Contexte et hypothèse

Les fronts océaniques sont caractérisés par de fortes discontinuités physiques (en termes de température, de salinité ou de nutriments ; Belkin *et al.* 2002; Scales *et al.* 2014a). Les processus physiques impliqués dans la formation de ces zones frontales permettent l'augmentation de la production primaire (Olson & Backus, 1985; Olson *et al.*, 1994), agrégeant entre autres du macrozooplancton gélatineux (Le Fèvre, 1986; Acha *et al.*, 2004), connu pour être la ressource principale de la tortue luth (Lutz & Musick, 1996). Le système frontal le plus impressionnant de l'Atlantique nord est le Gulf Stream, l'un des courants les plus dynamiques au monde (Schmitz & McCartney, 1993; Lozier *et al.*, 1995; Ducet *et al.*, 2000). Étant donné que le Gulf Stream, comme tous les autres fronts océaniques, agrège de la biomasse et notamment des méduses, on s'attend à ce que *la tortue luth cible le front du Gulf Stream durant sa migration post-ponte pour s'alimenter*. Bien que des associations entre les déplacements de la tortue luth de l'Atlantique nord et le Gulf Stream aient été précédemment suggérées (Lutcavage, 1996; Eckert *et al.*, 2006; Fossette *et al.*, 2010a; Dodge *et al.*, 2014), aucune étude n'a encore démontré une forte affinité pour cette structure en utilisant des données océanographiques dans la dimension horizontale et verticale.

6.2 Méthodologie

Les résultats de ce sixième chapitre sont issus du suivi satellitaire de 10 femelles adultes suivies depuis le site de Rémire-Montjoly entre 2014 et 2015 :

- Une tortue luth équipée en 2014 d'une balise SPLASH10-F-296A ;
- Et neuf tortues luths équipées en 2015 de balises 9000-SRDL.

Les données issues de ces deux types de balises ont fourni des informations sur leur dispersion et leur comportement de plongée. La méthode du *Temps de Résidence* (TR) a tout d'abord été utilisée pour identifier leurs zones d'alimentation potentielles. Une série de variables environnementales a ensuite été extraite depuis trois bases de données différentes (LOCEAN, Copernicus et CLS) afin de relier leur comportement de prospection alimentaire aux structures océanographiques dans les deux dimensions (la méthodologie est détaillée dans l'Annexe G) :

- Dans la dimension horizontale : température de surface (SST), hauteur d'eau (SSH), concentration en chlorophylle a, biomasse de micronecton, profondeur euphotique, Finite-Size Lyapunov Exponent (FSLE) pour l'identification de filaments ; les gradients issus des données de SST et SSH ont ensuite été calculés afin d'identifier les zones de fronts ;

- Dans la dimension verticale : profondeur de la couche de mélange, salinité de l'eau (profondeur de la halocline), profondeur du maximum de chlorophylle *a* (profondeur de la nutricline).

6.3 Zones d'alimentation côtières et océaniques

Les tortues luths de l'Est guyanais ont réalisé une migration longue et océanique vers l'Atlantique nord, parcourant en moyenne (± SD) 8577 ± 2842 km (min-max : 4957-12746 km) - Annexe G, Tableau 1. Tout comme la population de l'Ouest guyanais (Fossette *et al.*, 2010a,b; Ferraroli *et al.*, 2004), les dix femelles de l'Est ont migré vers les latitudes moyennes (> 30°N) et dans différentes directions, *i.e.* sud-est du plateau continental américain, Terre-Neuve-et-Labrador, à l'embouchure du fleuve Saint-Laurent, aux Açores, et même dans des eaux pélagiques de l'Atlantique nord (Figure 6.1a).

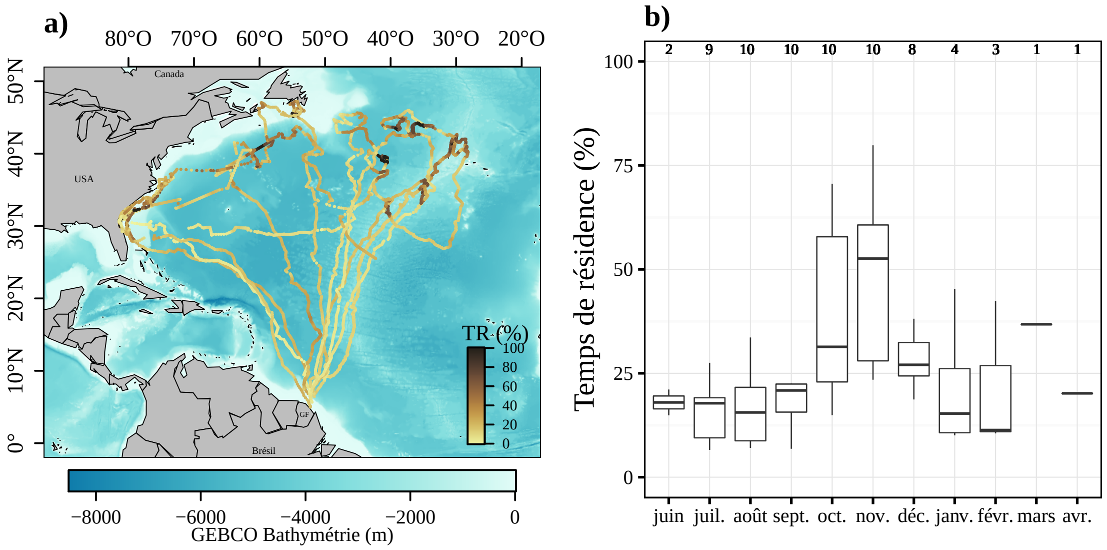


FIGURE 6.1 – **(a)** Proportion du Temps de Résidence (TR, en %) calculé le long des trajectoires des 10 tortues luths équipées en 2014 (n = 1) et 2015 (n = 9), et **(b)** boîtes à moustaches du TR (en %) en fonction des mois de suivi. Le TR (initialement exprimé en jours) a été converti en pourcentage à partir de la valeur maximale obtenue pour chaque individu pour obtenir une échelle comparable entre les individus. **(b)** les positions associées à chacune des valeurs maximales dans **(a)** sont considérées comme des zones d'alimentation potentielles. Guyane française (GF) correspond au point de départ et au site de déploiement des balises situé en Guyane française. Les numéros dans **(b)** situés en haut des boîtes à moustaches correspondent à la taille de l'échantillon pour chaque boîte à moustache, *i.e.* le nombre d'individus suivis par mois.

L'importance de ces zones d'alimentation pour cette espèce est renforcée par de précédentes études qui ont d'ores et déjà identifié ces mêmes zones clés (Fossette *et al.*, 2010a,b; Ferraroli *et al.*, 2004; Eckert *et al.*, 2006; James *et al.*, 2005). Les dix tortues luths ont quitté la Guyane française entre le mois de juin et la fin du mois d'août, occupant des zones associées à des TR élevés entre août et novembre (Figure 6.1b), et donc assimilées à des aires d'alimentation potentielles, aussi bien côtières qu'océaniques. La période de prospection alimentaire s'est donc principalement étendue d'octobre à décembre, car associée à un TR élevé.

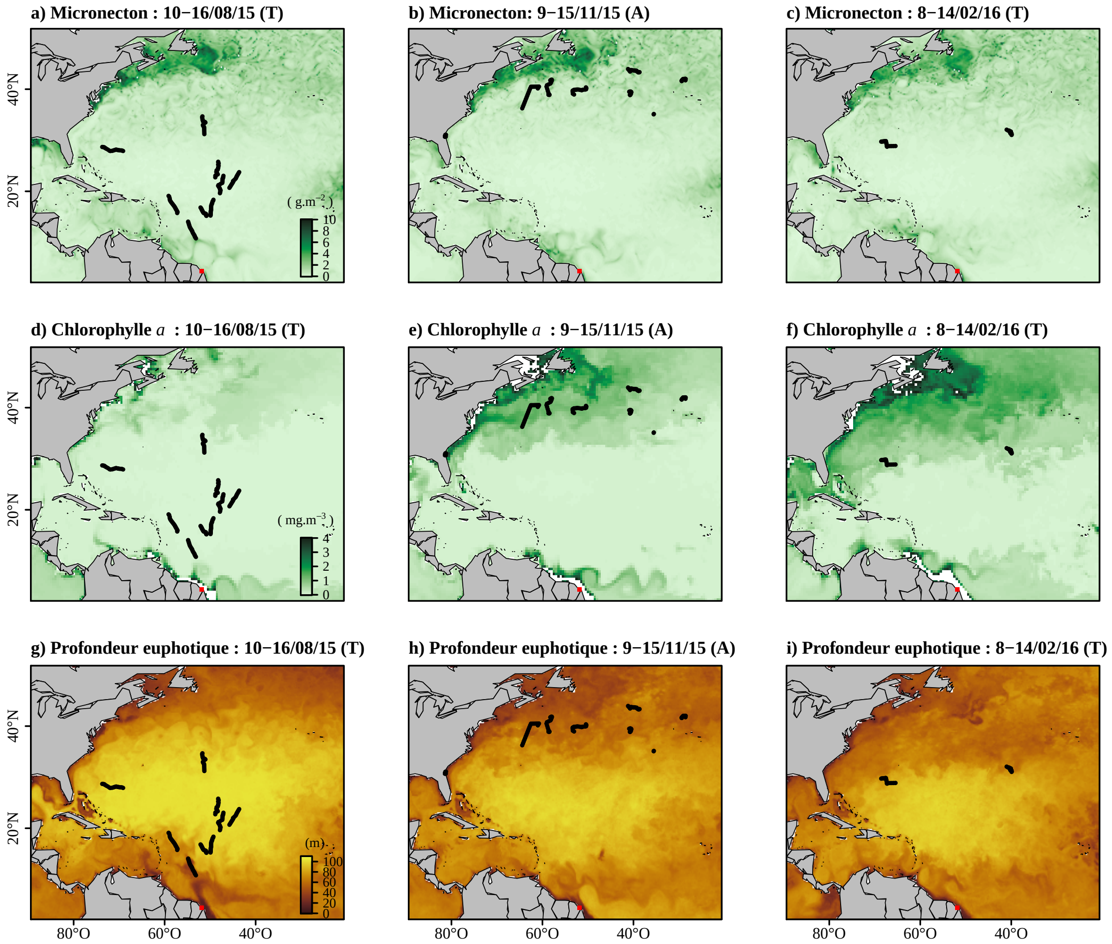


FIGURE 6.2 – Cartes hebdomadaires de la biomasse de micronecton prédite par SEAPODYM (**c**), de la concentration en chlorophylle *a* extraite de Copernicus (**d**, **e**, **f**), et de la profondeur euphotique prédite par SEAPODYM (**g**, **h**, **i**) pour trois périodes : (**a**, **d**, **g**, n = 10) le transit durant la traversée du gyre subtropical, (**b**, **e**, **g**, n = 10) la phase d'alimentation et de nouveau (**c**, **f**, **i**, n = 3) en transit. T correspond à 'Transit' et A à 'Alimentation'. Les points noirs correspondent aux positions des individus pour la semaine considérée, et le carré rouge au point de départ en Guyane française.

6.4 Sélection de zones riches en chlorophylle *a*

La première partie de la migration au sein du gyre subtropical Atlantique nord a été associée à des TR faibles (phases de transit) pour toutes les femelles suivies. Considérée comme un désert océanique (Tomczak & Godfrey, 2013; Marañón *et al.*, 2000), cette zone peu productive située au cœur de l'Atlantique nord a été associée à une faible concentration en chlorophylle *a* (Figure 6.2d) et une faible biomasse de micronecton (Figure 6.2a). La biomasse de micronecton a été significativement plus élevée dans les zones de TR élevé que dans les zones de transit (moyenne ± SE : 1,31 ± 0,25 *vs.* 0,56 ± 0,04 g.m^{-2}, respectivement, test de Wilcoxon : $p < 0{,}05$) - Figure 6.3a. De la même façon, la concentration en chlorophylle *a* a été significativement plus élevée durant les phases de TR élevé (moyenne ± SE : 0,53 ± 0,13 *vs.* 0,18 ± 0,04 mg.m^{-3}, respectivement, test de Wilcoxon : $p < 0{,}05$) - Figure 6.3b.

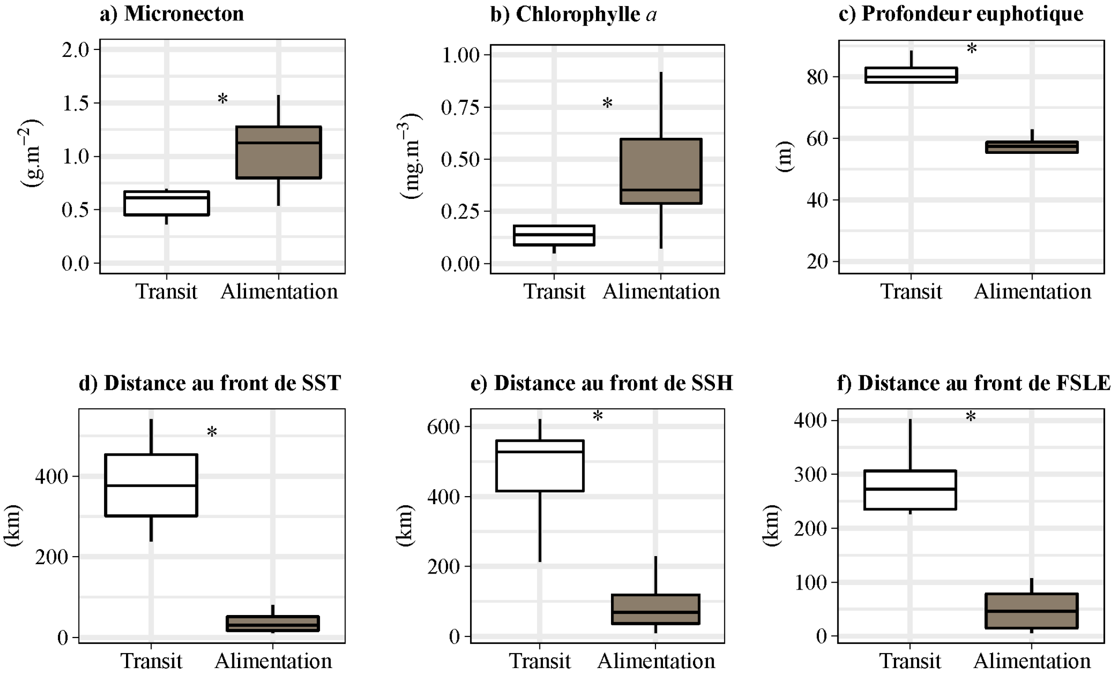


FIGURE 6.3 – Boîtes à moustaches de la biomasse de micronecton **(a)**, la concentration en chlorophylle *a* **(b)**, la profondeur euphotique **(c)**, la distance au front de SST le plus proche **(d)**, la distance au front de SSH le plus proche **(e)** et la distance au front de FSLE le plus proche **(f)**, à partir des données extraites en chacune des positions des individus pour les deux modes (transit en blanc et alimentation en gris). Les étoiles dans chaque figure indiquent une différence significative entre les deux modes. Le mode Transit est associé à un TR faible tandis que le mode Alimentation est associé à des valeurs plus élevées.

Les tortues luths ont donc concentré leur activité dans des zones productives (Figures 6.2b, 6.2e et 6.3b), situées dans les eaux tempérées des latitudes moyennes, où la concentration en chlorophylle *a* peut atteindre 1000 mg $C.m^{-2}.d^{-1}$ (Marañón *et al.*, 2000). Ces résultats concordent avec le comportement de la tortue luth du Pacifique (Bailey *et al.*, 2012a) et de l'Atlantique nord (Dodge *et al.*, 2014), pour lesquelles la probabilité de s'alimenter augmente avec la concentration en chlorophylle *a*.

La plupart des tortues ont toutefois migré vers le sud après avoir quitté leurs zones d'alimentation respectives (associé à un RT faible), restant ensuite dans des eaux riches en chlorophylle *a* (Figure 6.2f), mais plutôt pauvre en micronecton (Figure 6.2c). La profondeur de la couche euphotique a été significativement inférieure dans les zones de TR élevé (moyenne ± SE : 55,5 ± 4,8 *vs.* 77,9 ± 3,3 m ; test de Wilcoxon : $p < 0,005$), permettant un accès plus rapide à la ressource (Figures 6.2g, 6.2h, 6.2i et 6.3c). Cette hypothèse coïncide avec la distribution verticale du macrozooplancton gélatineux, qui est généralement concentré dans les couches de surface (Hays *et al.*, 2008).

6.5 Associations avec des fronts océaniques

En alimentation (TR élevé), les tortues luths ont traversé des eaux caractérisées par de forts gradients horizontaux, *i.e.* fronts de SST et de SSH (Figures 6.4b et 6.4e), et de fortes valeurs de FSLE (Figure 6.4h).

La distance au front de SST le plus proche a été significativement inférieure durant la phase d'alimentation que durant les phases de transit (moyenne ± SE : 37 ± 7,5 *vs.* 379 ± 32 km, test de Wilcoxon : $p < 0,005$) - Figures 6.3d et 6.4a, b et c. De la même façon, la distance au front de SSH le plus proche a été significativement inférieure en alimentation (moyenne ± SE : 86 ± 22 *vs.* 474 ± 44 km, test de Wilcoxon : $p < 0,005$) - Figures 6.3e et 6.4d, e et f. La distance au front de FSLE a été aussi significativement inférieure en alimentation (moyenne ± SE : 64 ± 22 *vs.* 253 ± 34 km, test de Wilcoxon : $p = 0,1094$) - Figures 6.3f et 6.4g, h et i.

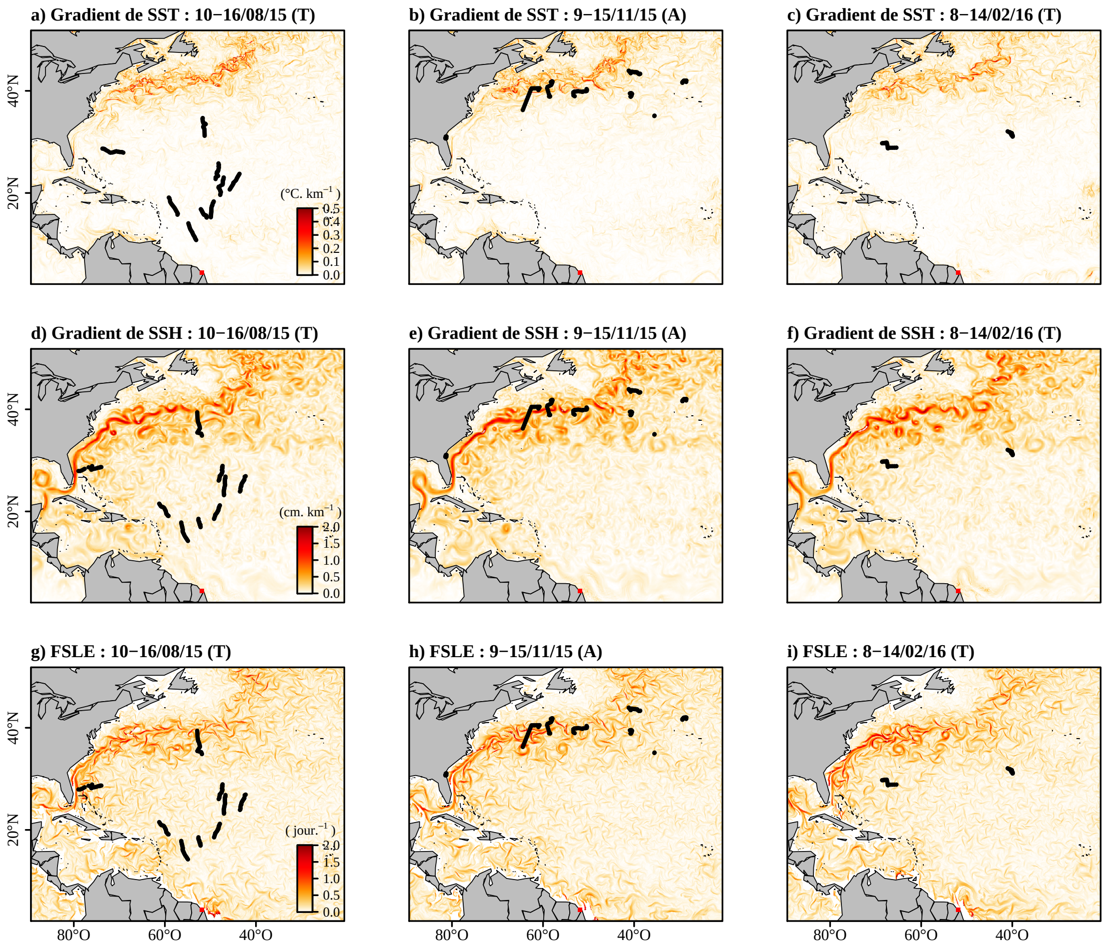


FIGURE 6.4 – Cartes hebdomadaires des gradients de SST (**a**, **b**, **c**), SSH (**d**, **e**, **f**) et FSLE (**g**, **h**, **i**) pour trois périodes : le transit durant la traversée du gyre subtropical (**a**, **d**, **g**, *n* = 10), la phase d'alimentation (**b**, **e**, **g**, *n* = 10) et de nouveau le transit (**c**, **f**, **i**, *n* = 3). T correspond à 'Transit' et A à 'Alimentation'. Les points noirs correspondent aux positions des individus pour la semaine considérée, et le carré rouge au point de départ en Guyane française.

Ces résultats signifient que les tortues luths ont ciblé des fronts océaniques pour s'alimenter. Les zones frontales correspondent à des eaux productives, car à l'interface de deux masses d'eaux aux propriétés contrastées (*e.g.* les eaux chaudes du Gulf Stream qui rencontrent les eaux froides du courant du Labrador), où le macrozooplancton gélatineux est susceptible de s'agréger (Sims & Quayle, 1998; Greer *et al.*, 2013; Powell & Ohman, 2015). De telles associations entre les fronts et les tortues marines (tortues caouannes et luths) ont déjà été documentées dans le Pacifique avec le courant Kuroshio (Polovina *et al.*, 2004, 2006; Polovina & Howell, 2005; Scales *et al.*, 2015), ou encore dans l'Atlantique avec le Gulf Stream (Eckert *et al.*, 2006; Fossette *et al.*, 2010a; Lutcavage, 1996; Witherington, 2002). Toutefois, jusqu'alors, seulement une étude avait démontré l'association entre les tortues luths adultes de l'Atlantique et le Gulf Stream à l'aide de données océanographiques (Dodge *et al.*, 2014), mais uniquement dans la dimension horizontale.

6.6 Variation du comportement de plongée

La profondeur maximale de plongée a varié significativement entre les individus (test de Kruskal-Wallis : p < 0,001), et 27% des plongées ont été réalisées dans les dix premiers mètres (Figure 6.5a). Les tortues ont plongé significativement plus profondément durant le transit (moyenne ± SE : 82,4 ± 5,6 *vs.* 38,5 ± 7,9 m, test de Wilcoxon : p < 0,005, Figure 6.5a), ce qui concorde avec le comportement de la population de l'Ouest guyanais (moyenne ± SD : 81,8 ± 56,2 *vs.* 53,6 ± 33,1 m, Fossette *et al.* 2010b), et pourrait notamment s'expliquer par les différents habitats exploités (côtiers *vs.* océaniques), et par conséquent la variabilité des proies consommées, *i.e.* du zooplancton gélatineux des profondeurs en pleine eau ou bien des Scyphozoaires des eaux de surface en zone côtière (James & Herman, 2001; Hays *et al.*, 2004b; Fossette *et al.*, 2010c).

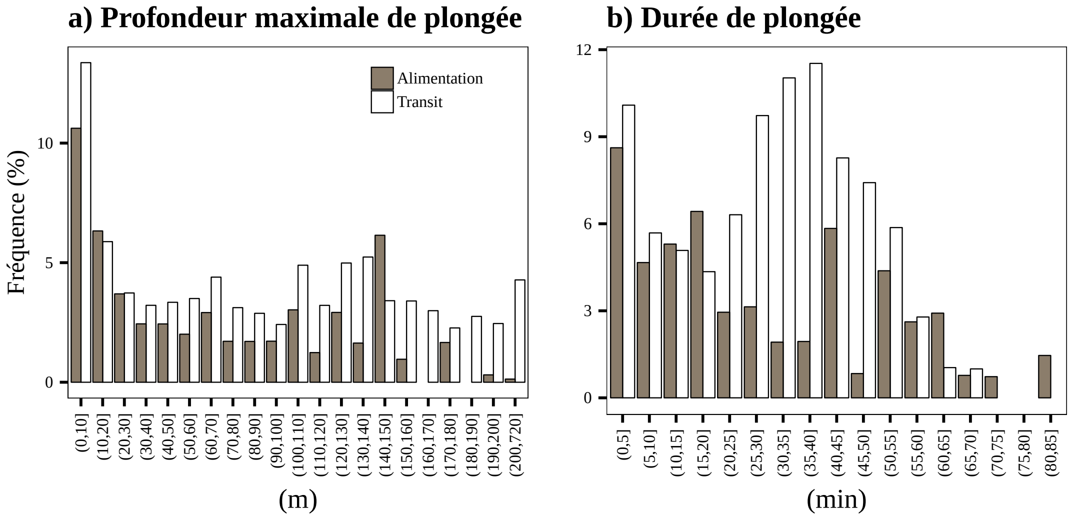


FIGURE 6.5 – Histogrammes de la profondeur maximale de plongée **(a)** et de la durée de plongée **(b)** des dix tortues luths équipées en 2014 (n = 1) et 2015 (n = 9) pour les deux modes (transit en blanc et alimentation en gris).

Concernant les durées de plongées, 26% d'entre elles ont duré moins de 10 min, et 31% entre 20 et 45 min (Figure 6.5b). Une variabilité interindividuelle a également été observée pour les durées de plongées (test de Kruskal-Wallis : p < 0,001), ce qui tend à confirmer cette importante plasticité comportementale chez cette espèce (Fossette *et al.*, 2007). Les tortues luths ont réalisé des plongées significativement plus courtes en alimentation (moyenne ± SE : 14,3 ± 2,4 *vs.* 27,0 ± 1,3 min, test de Wilcoxon : p < 0,005) - Figure 6.5b.

Parmi les 720 plongées enregistrées par les balises SRDL, 76% des temps de surface ont duré moins de 5 min (moyenne ± SE : 13,1 ± 2,4 min). Les temps de surface ont été significativement différents entre les individus (test de Kruskal-Wallis : p < 0,001), mais n'ont pas varié significativement selon le mode (moyenne ± SE : 12,9 ± 2,6 en transit *vs.* 11,3 ± 2,6 min en alimentation, test de Wilcoxon : p = 0,6523). Comme cela a pu être observé dans le nord-ouest de l'Atlantique (James & Mrosovsky, 2004), les temps de surface longs renforcent l'hypothèse que les individus nagent en surface pour consommer des proies de grande taille. Le TAD moyen (± SD) était de 0,59 ± 0,004, et la majorité des plongées était en V (85% et 4% en U), ce qui est commun chez cette espèce (Fossette *et al.*, 2008b).

6.7 Effet de la température

Les valeurs de SST et de température à la profondeur maximale atteinte par les tortues (TempProf) ont diminué au cours de la durée du suivi, avec les valeurs les plus élevées enregistrées au mois de juin (moyenne ± SE : 28,1 ± 0,3 et 27,6 ± 0,1 °C, respectivement), et les plus basses au mois de novembre (moyenne ± SE : 21,1 ± 3,1 et 20,7 ± 3,1 °C, respectivement) - Figure 6.6a.

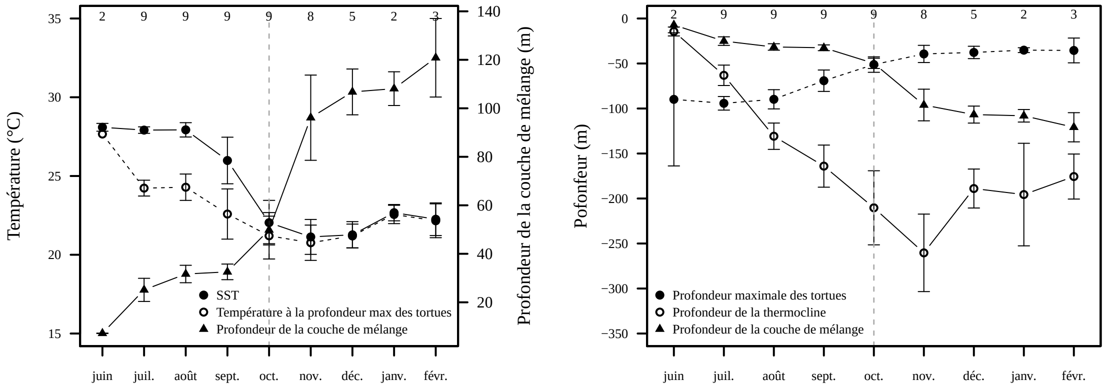


FIGURE 6.6 – **(a)** Moyennes mensuelles (± SE, extraites aux positions des tortues luths) de la SST (ronds pleins), de la température à la profondeur maximale atteinte par les individus (ronds vides,TempProf) et de la profondeur de la couche de mélange (triangles). **(b)** Moyennes mensuelles (± SE) de la profondeur maximale atteinte par les individus (ronds pleins), de la profondeur de la thermocline (ronds vides) et de la profondeur de la couche de mélange (triangles). La ligne pointillée verticale correspond au début de la phase d'alimentation et les chiffres en haut des figures à la taille de l'échantillon pour chaque mois.

La différence entre la SST et la TempProf a varié entre 0 et 6,2 °C, étant maximale en juillet (moyenne ± SE : 3,6 ± 1,4 °C), et minimale en février (moyenne ± SE : 0,09 ± 0,1 °C). La plus faible différence entre la SST et la TempProf a coïncidé avec l'approfondissement de la couche de mélange entre octobre et février (Figure 6.6a, Kara *et al.* 2003). La couche de mélange s'est approfondie entre août et novembre (moyenne ± SE :

31,6 ± 10,7 *vs.* 96,1 ± 49,7 m, respectivement) - Figure 6.6b. La thermocline s'est également approfondie de juin (9,4 m, $n = 1$) à novembre (moyenne ± SE : 260,3 ± 121,7 m), avant de remonter nettement par la suite (moyenne ± SE en février : 175,5 ± 43,3 m). En alimentation, les tortues luths sont restées dans la couche de mélange, au-dessus de la thermocline (Figure 6.6b). La couche de mélange est associée à un apport nutritif élevé en hiver (Kara *et al.*, 2003), ce qui explique par conséquent l'agrégation des tortues luths dans cette couche en hiver pour s'alimenter. À l'inverse, entre juin et octobre, durant le transit avant d'atteindre leurs zones d'alimentation, les individus ont majoritairement ciblé la thermocline, nageant en dessous de la couche de mélange (Figure 6.6b), dans des eaux plus froides. Un comportement similaire avait été observé chez la population de tortues luths de l'Ouest guyanais (Fossette *et al.*, 2010c), et pourrait être dû à la recherche de températures plus froides situées plus en profondeur afin d'économiser de l'énergie durant la migration.

6.8 Résumé

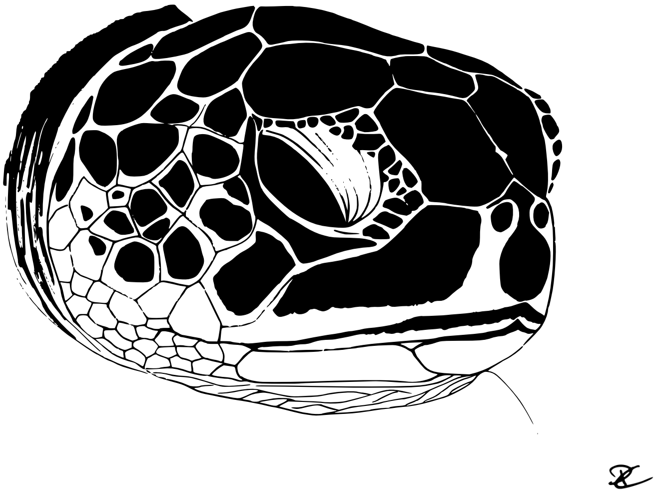
Bien que la tortue luth de l'Atlantique nord ait déjà fait l'objet de nombreux suivis télémétrique depuis la Guyane française (Fossette *et al.*, 2008a, 2010a, 2007, 2008b, 2010c; Ferraroli *et al.*, 2004), il s'agit de la première étude focalisée sur la population de l'Est guyanais, qui est génétiquement différente de la population de l'Ouest guyanais (Molfetti *et al.*, 2013) :

- Les tortues luths ont réalisé une longue migration océanique.
- Elles ont rejoint des zones d'alimentation côtières et océaniques situées dans les latitudes moyennes (> 30 °N).
- Bien qu'elles aient utilisé des aires d'alimentation différentes d'un point de vue géographique (situées entre 80-30 °O et 28-45 °N), elles ont ciblé une structure océanographique commune : le front du Gulf Stream.
- Les tortues luths ont ciblé des zones productives, riches en chlorophylle *a*.
- En alimentation, les tortues luths se sont associées à de forts gradients (de SST et de SSH) ainsi qu'à une couche de mélange profonde et riche en proies potentielles.

CHAPITRE 7

Discussion générale

Sommaire



7.1 Utilisation de l'habitat chez les femelles reproductrices

Le suivi satellitaire de ces 55 femelles gravides apporte des éléments nouveaux sur la manière dont ces animaux utilisent leur habitat pendant et en dehors de la période de reproduction (Tableau 7.1).

7.1.1 Bilan des connaissances acquises au cours de la thèse

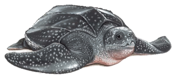
Le suivi en mer des trois espèces de tortues marines a ainsi permis de mettre en évidence une forte variabilité comportementale interspécifique, liée à différents facteurs tels que :

- Les traits reproducteurs, par exemple l'intervalle entre deux saisons de ponte ou l'intervalle entre deux pontes successives ;
- Les stratégies de reproduction : reproducteur sur capital ou reproducteur sur revenu ;
- La disponibilité alimentaire de l'habitat, qui va permettre ou non l'activité de prospection alimentaire ;
- Ou encore les adaptations physiologiques de ces espèces, telle que leur capacité de thermorégulation, qui va conditionner leurs déplacements.

Les traits reproducteurs

La durée de l'intervalle entre deux saisons de ponte (intervalle de migration) pourrait expliquer les différences observées dans le comportement migratoire des trois espèces. La distance parcourue au cours de la migration semble en effet corrélée à la durée de l'intervalle de migration chez la tortue olivâtre (moyenne ± SD : 1,7 ± 0,3 an), mais également chez la tortue verte et la tortue luth (moyenne ± SD : 2,8 ± 0,2 *vs.* 2,2 ± 0,1 ans, respectivement, Van Buskirk & Crowder 1994) - Tableau 7.1. Nos résultats indiquent en effet que les tortues olivâtres s'alimentent relativement à proximité de leur site de ponte durant leur migration (moyenne ± SD : 386 ± 291 km), comparées aux deux autres espèces (tortues vertes : 1799 ± 463 km et tortues luths : 3992 ± 2436 km). Par ailleurs, l'investissement lié à l'oviposition (c'est-à-dire au nombre de pontes par saison) détermine probablement la fréquence des retours à terre. En Guyane française, l'intervalle entre deux pontes successives chez les tortues olivâtres (28 jours, Plot *et al.* 2012) est plus important que celui observé chez les tortues vertes et les tortues luths, *i.e.* 13 *vs.* 10 jours (Girondot & Fretey 1996, Annexe A).

Tableau 7.1 – Synthèse des résultats issus des six articles publiés au cours de cette thèse. IP désigne la période d'inter-ponte.

	 **Olivâtre**	 **Verte**	 **Luth**
Surface du domaine vital en IP	423 km²	89-1620 km²	2552 km²
Fidélité au site de ponte	Forte	Forte	Forte
Types de plongées en IP	Variables	Coutes et peu profondes	Variables
Schéma migratoire	Court	Long	Long
Domaine utilisé en migration	Côtier	Côtier	Océanique & côtier
Aire de répartition en alimentation	Ceinture équatoriale	Ceinture équatoriale	Eaux tempérées
Habitat d'alimentation	Périphérie des tourbillons	Eaux claires et riches en herbiers	Fronts océaniques
Types de plongées en migration	Pélagiques/benthiques	Benthiques	Pélagiques
Structures verticales utilisées	Thermocline	-	Couche de mélange

Or, plus l'intervalle inter-ponte est faible, plus le nombre de pontes par saison est évidemment élevé (pour une saison de ponte de même durée). Une telle relation implique un investissement énergétique plus important pour les femelles gravides, ce qui peut expliquer les différences importantes de la durée des intervalles entre deux saisons de reproduction observées entre ces trois espèces, mais également entre les deux sexes. En effet, contrairement aux femelles, les mâles n'ont évidemment pas à investir l'énergie nécessaire à l'oviposition, ce qui leur permet par conséquent de se reproduire chaque année (Hays *et al.*, 2014). À l'inverse, la plupart des femelles ne se reproduisent que tous les 2 à 4 ans afin de reconstituer leurs réserves corporelles, comme cela a été observé chez certaines espèces de Pétrels et d'Albatros (Chastel *et al.*, 1995; Nevoux *et al.*, 2007).

Les stratégies de reproduction

Bien que les tortues marines aient longtemps été considérées comme des reproducteurs sur capital cessant de s'alimenter durant la saison de reproduction (Drent & Daan 1980; Goldberg *et al.* 2013; Perrault *et al.* 2014, Chapitre 1), de récentes études indiquent qu'elles peuvent également se nourrir au cours de l'inter-ponte (Hays *et al.*, 2002b; Schofield *et al.*, 2006; Georges *et al.*, 2007). Dans ce cas précis, elles adopteraient par conséquent une stratégie de reproducteur sur revenu, voire une stratégie intermédiaire, comme cela a été suggéré par Fossette (2008). L'investissement parental étant inexistant chez les Chéloniens, il peuvent allouer toute l'énergie uniquement aux déplacements et à la reproduction (Bonnet *et al.*, 1998), une stratégie similaire à celle observée chez le serpent *Acrochordus arafurae* (Shine, 1985). Le métabolisme bas de ces ectothermes limite ainsi la dépense énergétique (Pough, 1980, 1983). Le fait que durant toute leur période de ponte les tortues marines de Guyane française restent à proximité du site de ponte et réalisent des plongées très courtes et peu profondes contribue à cette stratégie d'économie d'énergie (Tableau 7.1, Annexes A et B).

La disponibilité alimentaire de l'habitat

Si les conditions locales de l'habitat le permettent, les tortues marines adoptent une stratégie de reproducteur sur revenu en s'alimentant durant cette période coûteuse en énergie. Le comportement de plongée des tortues olivâtres suggère une activité de prospection alimentaire des individus au cours de la saison de ponte. Dans les mêmes zones où nos travaux montrent que ces tortues s'agrègent durant cette période, leurs proies potentielles sont disponibles d'après les relevés d'épifaune réalisés la même année par l'Ifremer sur le plateau continental guyanais (43% de crustacés et 39% de poissons, Annexe B). Ces proies échantillonnées correspondent en effet à celles observées dans les contenus stomacaux des tortues olivâtres étudiées au cours de la période de reproduction au Brésil

(Colman *et al.*, 2014). Par ailleurs, la présence de méduses le long des côtes guyanaises révélée par un échantillonnage réalisé par l'IFREMER entre 2005 et 2006 (Fossette *et al.*, 2009) permettrait d'étayer l'hypothèse selon laquelle les tortues luths pourraient également se nourrir durant la saison de ponte. À la différence de la tortue olivâtre et de la tortue luth, il est par contre peu probable que la tortue verte de Guyane française puisse s'alimenter durant l'inter-ponte du fait que la zone où elle se trouve est dépourvue de phanérogames et d'algues marines. Son régime alimentaire étant principalement herbivore à l'âge adulte, elle adopte vraisemblablement une stratégie de reproducteur sur capital, en réalisant des plongées benthiques de repos, tout en restant à proximité du site de ponte afin de limiter ses déplacements (Annexe A). On ne peut cependant exclure qu'elle tire profit de la présence de méduses et de crustacés le long des côtes guyanaises, sans avoir à réaliser des déplacements importants. Un tel comportement omnivore a été montré chez les tortues vertes du Pacifique, à la fois sur des habitats côtiers (Lemons *et al.*, 2011) et océaniques (Hatase *et al.*, 2006; Lemons *et al.*, 2011). Ce changement de comportement alimentaire durant la saison de ponte pourrait être lié à la faible densité de phanérogames marines et à une faible diversité algale dans le Pacifique, contrebalancée par une abondance de ressources d'origine animale, *i.e.* invertébrés mobiles et sessiles, organismes planctoniques, etc.

Les adaptations physiologiques

Tout comme la plupart des reptiles, les tortues marines ont la capacité de maintenir un différentiel thermique entre leur température corporelle et la température de leur environnement (Avery, 1982). Dans ce contexte, leurs déplacements en mer devraient être fortement influencés par les variations thermiques de l'environnement, et ce, dans les deux dimensions (horizontale et verticale). Une adaptation physiologiques toute particulière comme la thermorégulation pourrait expliquer que l'aire de répartition de la tortue luth en migration atteigne les latitudes arctiques (Annexe G). Parmi les sept espèces de tortues marines, la tortue luth a la capacité de réguler sa température corporelle interne (thermorégulation) en jugulant la déperdition thermique en fonction de son environnement, ce qui lui permet d'exploiter les eaux froides situées dans les latitudes tempérées voir subpolaires. D'après les travaux de Paladino *et al.* (1990), un élément clé permettant à la tortue luth de maintenir une température corporelle élevée dans des eaux froides serait sa très grande taille, et donc une surface de déperdition réduite par rapport à son volume producteur de chaleur, d'où le concept de "gigantothermie". Les tortues luths peuvent ainsi maintenir une différence de 18 °C (Frair *et al.*, 1972) entre leur température corporelle (25,5 °C) et la température ambiante, soit pour se réchauffer dans les eaux froides (7,5 °C), soit pour se refroidir à terre (lors de l'oviposition) ou à la surface de l'eau dans les tropiques. Les tortues marines à écailles ont également cette capacité physiologique, mais elle est très inférieure à celles des tortues luths (*e.g.* tortue caouanne : 0,7-1,7 °C, Sato *et al.* 1995 ; tortue verte : 1-3 °C, Mrosovsky 1980; Standora *et al.* 1982; Sato *et al.* 1998), ce qui explique que ces espèces soient majoritairement distribuées dans des eaux tropicales et subtropicales (UICN, Tableau 7.1, Annexes D, E et F).

7.1.2 Limites et perspectives scientifiques

Durée d'émission des balises

L'une des limites de nos travaux est l'insuffisante durée d'émission de certaines balises, ce qui a limité le suivi à long terme de la migration. Ces faibles durées d'émission, notamment chez la tortue olivâtre (Annexe F), peuvent en partie s'expliquer par la très faible couche de kératine sur la carapace de cette espèce (Whiting *et al.*, 2007), ce qui empêche le nettoyage complet de sa dossière pour permettre une bonne adhérence de la colle Epoxy. Toutefois, la cause la plus probable de la faible durée d'émission des balises est vraisemblablement la capture accidentelle des tortues dans les filets de pêche le long du plateau des Guyanes (Fossette *et al.*, 2014b). En effet, en raison de son aire de répartition et de son régime alimentaire à base de crustacés, la tortue olivâtre est particulièrement touchée par ce fléau dans cette région en raison du grand nombre de crevettiers (Gueguen, 2000).

Étude l'indice de la condition corporelle

Le déploiement simultané sur un grand nombre d'individus de loggers composés d'un GPS, d'un accéléromètre 3D, d'un gyromètre, d'un magnétomètre et de capteurs de pression et de température permettrait d'enregistrer à la fois les trajectoires des tortues et leur comportement de plongée à fine échelle durant un cycle complet d'inter-ponte (soit 28 jours pour les olivâtres, 13 jours pour les vertes et 10 jours pour les luths), et d'étudier l'évolution de la condition corporelle, comme cela a été réalisé chez l'éléphant de mer austral (Biuw *et al.*, 2003; Richard *et al.*, 2014). Il serait également intéressant d'estimer la durée nécessaire pour reconstituer les réserves corporelles des femelles adultes durant la migration, et de relier cette durée à l'intervalle de migration de chacune des trois espèces. Les travaux de Richard *et al.* (2014) ont récemment montré que la densité corporelle de l'éléphant de mer austral décroit au cours de son trajet en mer. L'explication est qu'en s'alimentant, l'éléphant de mer augmente donc sa proportion de lipides, ce qui augmente également sa flottabilité et le rend moins dense. On peut donc s'attendre à des résultats similaires pour les tortues marines.

Étude de l'indice de l'activité de prospection alimentaire et de la prise alimentaire

Une autre limite de ces travaux est la difficulté à valider l'indice de l'activité de prospection alimentaire en raison de la résolution trop faible des données collectées. Compte tenu de la durée importante des migrations (2 à 3 ans, Miller 1997), nous devions trouver un compromis entre la durée de vie de la batterie et le nombre de données transmises. Les données issues des dix tortues luths équipées en 2015 illustrent cette limite puisqu'une durée d'émission relativement longue a été enregistrée au détriment d'un nombre très limité de plongées (< 1 profil par jour, Annexe G). Cette faible résolution des données contraint nécessairement à l'utilisation d'indices de prospection alimentaire (*e.g.* first passage time, residence time ou hunting time), qui bien souvent, ne peuvent être validés a posteriori. Le déploiement de caméras associées à des loggers (cités précédemment) au cours de l'interponte permettrait de valider la méthode du *Hunting time* développée par Heerah *et al.* (2014) et de l'appliquer par la suite aux données basse résolution durant la migration des tortues marines. Cette approche combinée permettrait aussi d'estimer un indice de la prise alimentaire sur la base de la méthodologie employée chez les lions de mer de Steller (Viviant *et al.*, 2010). Une récente collaboration entre l'IPHC-DEPE et l'Aquarium La Rochelle a permis la réalisation d'une étude expérimentale (stage de Lorène Jeantet, ENSAT) en bassin sur trois espèces de tortues marines (tortue imbriquée, tortue verte et tortue caouanne). Les premiers résultats de cette étude ont permis de construire un arbre de décision et d'identifier une série d'activités associées à des signaux accélérométriques. Le second objectif sera (1) de comparer les signaux enregistrés en bassin à ceux obtenus par les tortues en milieu naturel et (2) d'équiper ces mêmes espèces de caméras et de loggers afin de lier les signaux accélérométriques aux activités réalisées par les individus en Guyane.

7.1.3 Perspectives en appui à la conservation

Les résultats obtenus au cours de cette thèse fournissent une base scientifique permettant de répondre à différents objectifs fixés par le Plan National d'Actions (PNA) en faveur des Tortues Marines de Guyane. Initié en 2003, le PNA de Guyane comprend un premier volet "Inventaire et diagnostics" qui synthétise l'état des connaissances sur les tortues marines de Guyane et sur les menaces qui pèsent sur ces trois espèces, puis un second volet "Plan d'Actions", définissant des objectifs sur cinq ou dix ans, accompagnés de fiches actions concrètes, hiérarchisées et chiffrées. Cette thèse répond à deux des sept grands objectifs fixés par le second PNA 2014 à 2023 (Entraygues, 2014), à savoir (1) la *réduction des menaces* et (2) l'*amélioration des connaissances au service de la conservation*.

Localiser les menaces en mer

Parmi les menaces qui pèsent sur les tortues marines à proximité de la Guyane, la pêche côtière artisanale et industrielle semble être la principale. Parmi les navires évoluant dans les eaux guyanaises, 60% se sont révélées correspondre à des embarcations étrangères, principalement surinamaises et brésiliennes (Levrel, 2012). L'apparition de cette pêche illégale est liée au fait que les eaux guyanaises sont plus poissonneuses et à la difficulté de l'Action de l'État en Mer (AEM) à contrôler tous les navires, compte tenu de l'importante surface maritime à couvrir (Levrel, 2012). La position des navires contrôlés et/ou déroutés lors des actions des autorités maritimes entre 2002 et 2012 indique qu'ils se concentrent à proximité des côtes, et notamment près des deux sites de ponte de Guyane française (Figure 7.1), favorisant par conséquent les interactions potentielles avec les femelles reproductrices au cours de l'inter-ponte, mais également durant la migration post-ponte (côtière) des tortues vertes en direction du Brésil (Chapitre 5 et Annexes D et E).

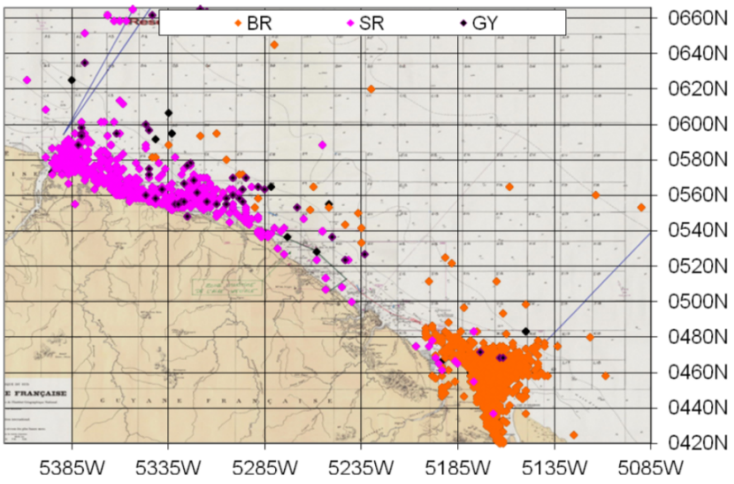


FIGURE 7.1 – Positions des navires contrôlés et/ou déroutés lors des actions des autorités maritimes entre 2002 et 2012. Carte issue de Levrel 2012.

Réduire les menaces en mer

Le PNA tortues marines de Guyane a listé plusieurs actions visant à réduire les menaces liées à pêche illégale aux filets maillants dérivants via (Entraygues, 2014) :

- La favorisation de la réponse pénale et administrative dans l'Ouest ;
- Le développement d'une coopération transfrontalière avec les pêcheurs des pays voisins ;

- L'optimisation de l'action de l'AEM dans l'Ouest ;
- La programmation d'interventions conjointes des Services Mixtes de la Police de l'Environnement (SMPE) avec la Réserve Naturelle de l'Amana ;
- Et l'amélioration des moyens de lutte contre la pêche illégale dans l'Ouest.

En plus des actions listées précédemment, le PNA tortues marines de Guyane vise également à déterminer le nombre de captures accidentelles dues à la pêche légale grâce à la mise en place d'observateurs à bord des navires. De tels contrôles permettraient également de réaliser des prélèvements de tissus dans le cadre d'études génétiques visant à une meilleure compréhension de la distribution des tortues marines aux différents stades (adultes et juvéniles) et de connaître leurs origines. Dans le cadre d'une étude réalisée par l'Université de Bretagne Occidentale (UBO) via des observateurs embarqués, le nombre de captures accidentelles annuelles de tortues olivâtres par les chalutiers a été estimé à 1000 individus durant les années 1990. De part sa petite taille, son mode de vie majoritairement benthique durant l'inter-ponte et son régime alimentaire carnivore, la tortue olivâtre est inévitablement l'espèce la plus touchée par la flottile crevettière (Gueguen, 2000). Face à ce constat alarmant, un système d'exclusion des tortues marines (TTED : *Trash and Turtle Excluder Device*) a été adopté et rendu obligatoire sur les chaluts crevettiers en Guyane française depuis 2010, afin de limiter le nombre de prises accidentelles.

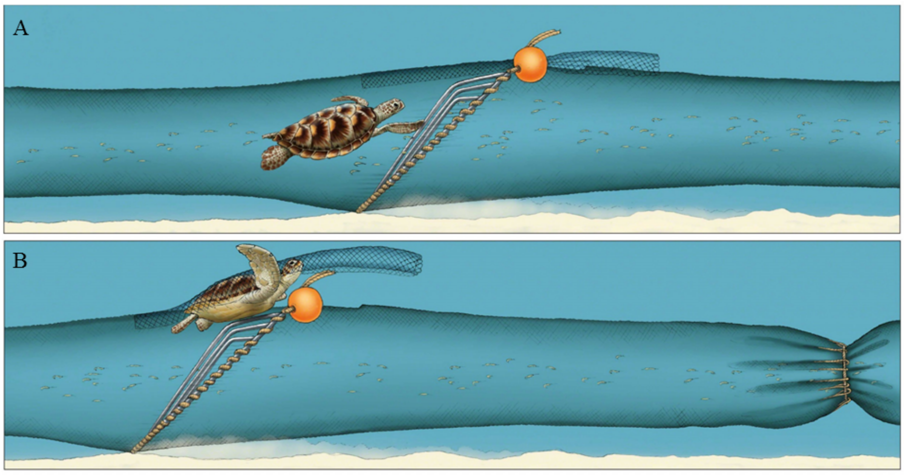


FIGURE 7.2 – Schéma illustrant le principe d'exclusion d'un TED. Schéma inspiré de Marc Dando.

Ce dispositif est adaptable aux chaluts et pourvu d'une grille métallique permettant l'exclusion de nombreuses espèces de mégafaune marine, dont notamment les tortues marines. Comparé au premier dispositif mis en place dans plusieurs pays depuis une trentaine d'années (le TED : *Turtle Excluder Device* ; *e.g.* Robins-Troeger 1994; Brewer *et al.* 1998, 2006), le TTED (Figure 7.2) dispose d'un espacement entre les barreaux (5 cm) plus réduit que ceux du TED (10,2 cm), ce qui permet de limiter davantage le nombre de prises accidentelles (Nalovic, 2013). Le suivi de la bonne mise en place de ce dispositif passera par des contrôles de l'AEM, mais aussi par la réalisation d'une enquête ou d'entretiens avec les pêcheurs.

Estimer les interactions entre les navires de pêche et les tortues marines

Après avoir identifié et localisé les menaces en mer, il est fondamental d'évaluer leur impact sur les déplacements des tortues marines au niveau spatiotemporel et dans les deux dimensions (horizontale et verticale). Pour faire suite aux études déjà menées dans l'océan Pacifique (*e.g.* Donoso & Dutton 2010; Lewison *et al.* 2004), l'océan Indien (*e.g.* Bourjea *et al.* 2008, 2014) et l'océan Atlantique (*e.g.* Lewison *et al.* 2004; Ferraroli *et al.* 2004; Fossette *et al.* 2014b), les résultats issus de cette thèse pourront contribuer à la définition des interactions spatiales entre les navires de pêche illégaux et les zones fréquentées par les tortues marines en Guyane, via le croisement des données de suivi télémétrique des individus avec les données géolocalisées des navires (données issues de l'AEM) au cours de la période de reproduction.

L'étude de Fossette *et al.* (2014b) à l'échelle du bassin Atlantique a permis d'identifier les zones potentielles de prise accidentelles des tortues luths selon trois degrés d'interaction : faible, moyen et élevé. Neuf zones avec une interaction "élevée" entre les navires de pêche et les tortues luths ont ainsi pu être identifiées. Elles sont situées à la fois dans des eaux internationales et dans des zones exclusives économiques (ZEE) de 12 pays : Cap Vert, la Gambie, la Guinée-Bissau, la Mauritanie, le Sénégal, les îles Canaries, les États-Unis, le Sahara occidental, l'Angola, le Brésil, la Namibie et l'île d'Ascension. Bien qu'apportant des informations capitales sur les zones concernées par une pression de pêche élevée à l'échelle du bassin Atlantique, cette étude ne fait pas état de la situation des autres espèces de tortues marines présentes dans cette région, notamment la tortue verte et la tortue olivâtre de Guyane. L'utilisation des données analysées au cours de cette thèse permettra ainsi de réaliser une méta-analyse des trois espèces étudiées, et ce, dans les deux dimensions (horizontale et verticale), en combinant le comportement de plongée des individus et les paramètres liés à l'activité de pêche (profondeur et longueur des filets, durée de cale des filets déployés, taille des mailles des filets, durée en mer des navires, etc). Cette approche permettra d'obtenir une cartographie fine des interactions, dans les deux dimensions, entre les tortues marines de Guyane et les filets de pêche. Les résultats obtenus permettront d'identifier des zones de protection à prioriser durant la saison de reproduction des tortues marines et d'appuyer la mise en place de mesures de gestion adaptées pour limiter les interactions avec les navires de pêche. Il est important de rappeler que cette interaction est également problématique pour les professionnels de la pêche, ce qui implique que cette étude soit impérativement menée en concertation avec eux.

7.2 Utilisation de l'habitat chez les immatures

Les déplacements des tortues marines immatures ont été peu étudiés et il est impératif de comprendre comment ces individus utilisent leur habitat durant les différentes phases de leur cycle de vie dans l'océan Atlantique et dans les Caraïbes.

7.2.1 Lien entre habitat de développement et site de reproduction

Comme vu précédemment dans le Chapitre 1, différentes techniques existent à ce jour pour étudier la dispersion en mer des tortues marines : (1) le suivi satellitaire, (2) la génétique ou encore (3) la méthode de Capture-Marquage-Recapture (CMR).

Suivi satellitaire

Depuis les années 2000, plusieurs études utilisant le suivi satellitaire ont permis de compléter les connaissances sur l'écologie en mer des tortues marines immatures dans l'océan Indien (Dalleau *et al.*, 2014), l'océan Pacifique (Polovina *et al.*, 2001, 2000; Howell *et al.*, 2010), ou encore l'océan Atlantique (Godley *et al.*, 2003; Mansfield *et al.*, 2009). Mais à ce jour, très peu d'études ont établi le lien entre les habitats de développement des juvéniles et les sites de reproduction et/ou d'alimentation des adultes à l'aide du suivi satellitaire. Une étude en cours menée par notre institut de recherche (l'IPHC-DEPE), portant sur le suivi satellitaire de tortues vertes juvéniles et imbriquées des Caraïbes suggère une connectivité entre les habitats (de reproduction et d'alimentation) des adultes venant pondre en Guyane et l'habitat de développement des juvéniles situé en Martinique (Annexe H et Figures 7.3 et 7.4).

Sur les 12 individus immatures équipés de balises Argos en Martinique en 2015 et 2016, neuf ont quitté leur habitat de développement, et on réalisé des migrations multidirectionnelles à travers la région Atlantique-Caribéenne (Figures 7.3 et 7.4, Annexe H). Tandis que cinq individus se sont dirigés vers la Floride, les îles vierges américaines, Panama, les îles Caïmans, ou encore le Ghana, quatre ont migré vers le sud-est, en direction des zones d'alimentation des états de Ceará et Rio Grande do Norte au Brésil (Figure 7.3), où séjournent les femelles adultes de Guyane française entre deux saisons de ponte (Annexe E).

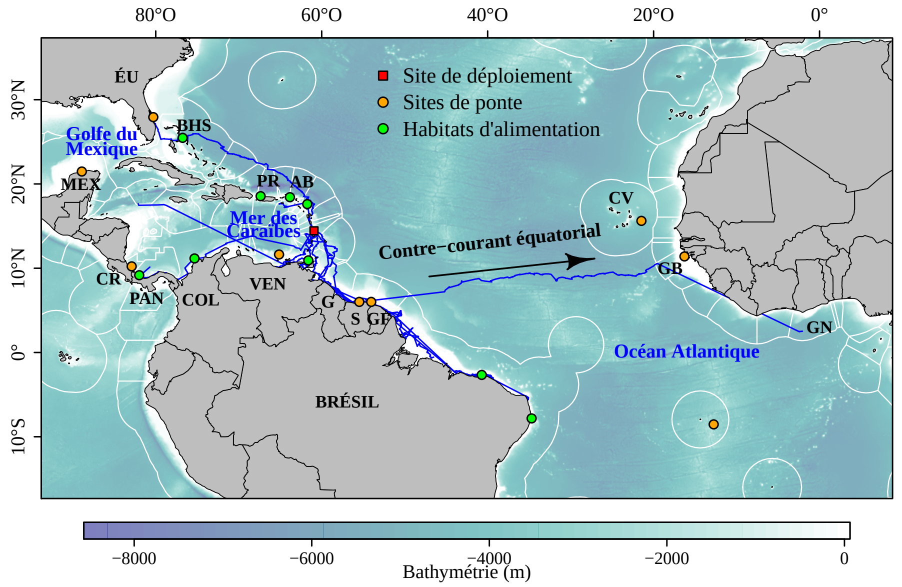


FIGURE 7.3 – Trajectoires des neuf tortues vertes immatures parties en migration depuis leur habitat de développement en Martinique. Les contours blancs correspondent aux différentes ZEE traversées : AB (Antigua-et-Barbuda), BHS (Bahamas), COL (Colombie), CM (îles Caïmans), CR (Costa Rica), CV (Cap Vert), ÉU (États-Unis), GB (Guinée-Bissau), G (Guyana), GF (Guyane française), GN (Ghana), MEX (Mexique), PAN (Panama), PR (Puerto Rico), VEN (Venezuela), S (Suriname).

Les différences morphométriques entre les tortues vertes qui n'ont pas migré (moyenne ± SD : 74,9 ± 9,6 cm) et les migratrices (moyenne ± SD : 84,3 ± 3,5 cm) suggèrent que les individus entament leur migration après avoir atteint leur maturité sexuelle, soit pour explorer d'autres habitats de développement (Carr *et al.*, 1978), soit pour rejoindre les zones d'alimentation et/ou de reproduction des adultes. Dans ce contexte, nous pouvons supposer qu'une partie de la population d'immatures résidant dans les zones de développement martiniquaises pourrait être originaire de la Guyane française, du Suriname ou du Brésil. Nous supposons qu'une fois la maturité sexuelle atteinte, ces individus rejoignent les zones d'alimentation brésiliennes, communes à celles des femelles adultes venant pondre en Guyane française (Annexes D et E), et y séjournent durant plusieurs années jusqu'à ce qu'elles aient atteint la taille moyenne (± SD) de 112,7 ± 6,3 cm (CCL), soit la taille moyenne des femelles gravides venant pondre en Guyane (Annexe A). Les analyses génétiques (en cours de réalisation), réalisées sur les tortues vertes de Martinique permettront d'étayer l'hypothèse selon laquelle (1) les immatures présents sur les zones de développement de Martinique pourraient être en grande partie originaires des sites de ponte situés entre le Suriname et le Brésil, et (2) lorsqu'ils ont atteint la maturité sexuelle, les individus séjourneraient plusieurs années sur les zones d'alimentation communes aux adultes, avant de se reproduire.

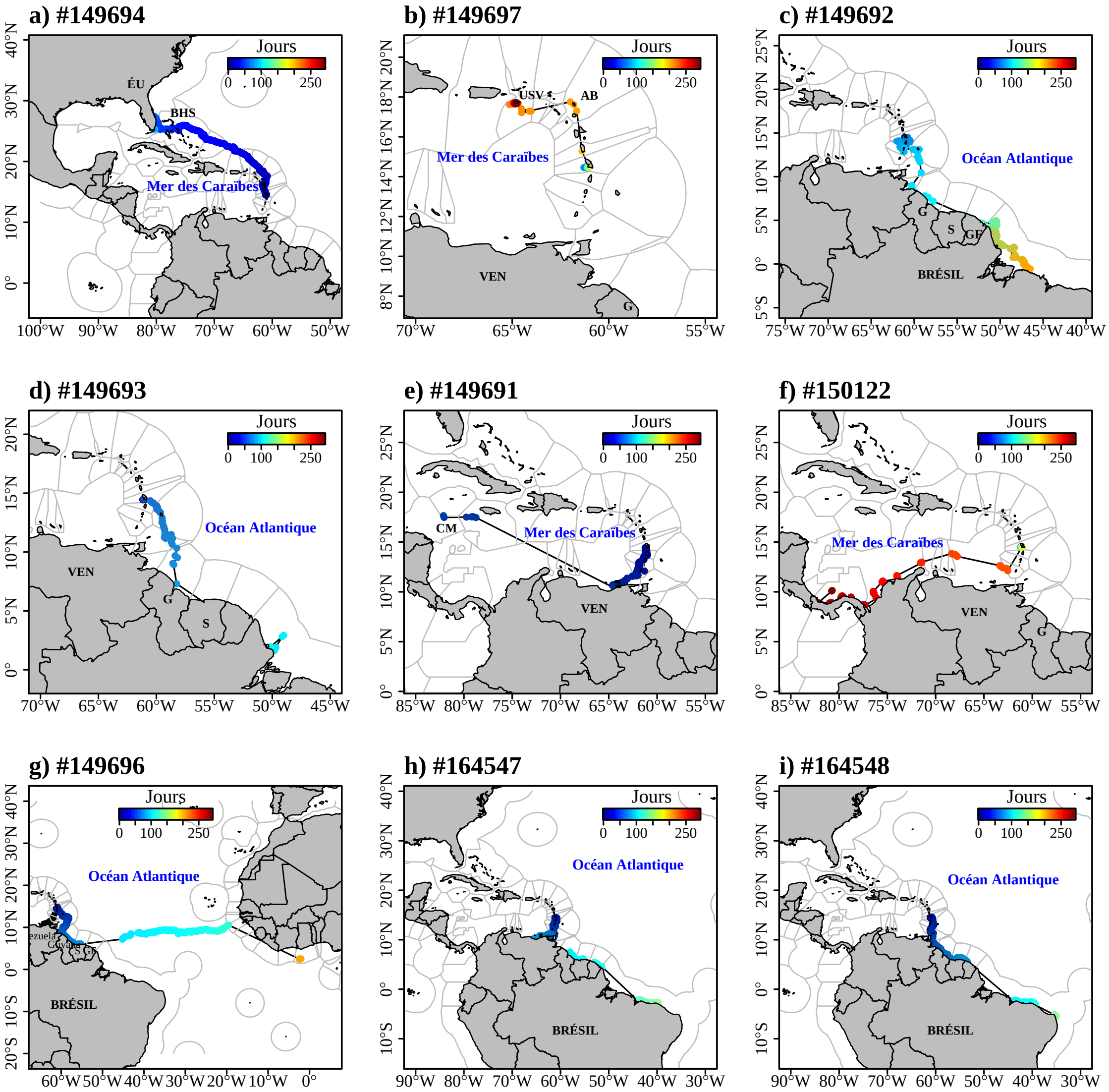


FIGURE 7.4 – Trajectoires (lignes noires) et positions (points en couleur) des neuf tortues vertes immatures parties en migration depuis leur habitat de développement en Martinique.

Analyses génétiques

Pour compléter ces premiers résultats, une analyse génétique qui est en cours permettra d'identifier les origines natales de près de 161 individus issus de Martinique, dont les neuf migrateurs, en comparant leur ADN mitochondrial à celui de cinq populations de l'Atlantique occidental : Guadeloupe, Suriname (Galibi, estuaire du Maroni), Yalimapo (estuaire du Maroni, Guyane), Cayenne (Guyane) et Brésil (São Francisco de Itabapoana). Nous nous attendons à ce que les résultats issus de cette analyse confirment les données issues du suivi satellitaire (Annexe H), à savoir qu'une proportion importante des tortues présentes sur les zones de développement de Martinique soient issues des populations de Guyane française, du Suriname et du Brésil. Ces données confirmeraient alors que la région Atlantique-Caraïbes est un lieu d'un important brassage génétique, comme cela avait déjà été évoqué par de précédentes études réalisées sur d'autres îles des Caraïbes (Bass *et al.*, 2006; Bass & Witzell, 2000; Luke *et al.*, 2003).

Toutefois, nous nous attendons à ce qu'une partie des individus échantillonnés en Martinique restent d'origine inconnue. En effet, pour le moment nous ne disposons pas des données d'ADN mitochondrial des autres populations de tortues vertes de l'Atlantique (Amérique Centrale, Afrique de l'Ouest et Centrale, etc.). En confrontant la littérature à nos données de suivi satellitaire, ces individus pourraient notamment provenir de l'île de l'Ascension (Luke *et al.*, 2003), ou encore de la côte ouest de l'Afrique (Monzón-Argüello *et al.*, 2010; Jordao *et al.*, 2017, 2015), ce qui pourrait expliquer la migration jusqu'en Afrique de l'Ouest d'un des neuf individus équipés (Figure 7.4g). Une étude similaire (de suivi satellitaire et de génétique) portant sur des tortues imbriquées (juvéniles et adultes) en Martinique est également en cours d'analyse (Annexe I), et permettra d'identifier la provenance de ces individus, et de confirmer l'important brassage génétique de la région Caribéenne. Dans ce contexte, la comparaison de l'ADN mitochondrial des individus de Martinique à celui d'autres populations de l'Atlantique occidental s'avère donc nécessaire pour mieux comprendre les schémas de dispersion des tortues marines avant la période de reproduction.

Suivi Capture-Marquage-Recapture (CMR)

En complément du suivi satellitaire et de la génétique, la méthode de CMR permet d'obtenir un suivi à long terme des animaux marqués grâce aux bagues et/ou transpondeurs RFID sous-cutanées. La méthode de CMR est utilisée depuis plus de 40 ans en Guyane et son usage a été initié en Martinique en 2009. Grâce à un marquage simultané sur les zones de développement en Martinique et sur les sites de ponte en Guyane, la CMR permettra d'identifier les femelles reproductrices ayant déjà été marquées en Martinique plusieurs années auparavant. Les tortues vertes immatures (de Martinique) qui se rendent sur les zones d'alimentation des adultes au large du Brésil pourraient revenir d'ici quelques années en Guyane pour se reproduire et/ou pondre (s'il s'agit de femelles) pour la première fois. Compte tenu de la différence morphologique entre les tortues vertes migratrices parties de Martinique (moyenne ± SD : 84,3 ± 3,5 cm) et les tortues gravides de Guyane (moyenne ± SD : 112,7 ± 6,3 cm; min-max : 91-148 cm, n = 1855), on suppose que ces immatures achèvent leur croissance durant quelques années dans les habitats d'alimentation des adultes au Brésil, jusqu'à atteindre une taille proche de celles des tortues gravides de Guyane, avant d'entreprendre leur migration prénuptiale vers les zones de reproduction de la Guyane.

Les études menées sur les individus immatures (subadultes) des Caraïbes nous apportent ainsi des premiers éléments de réponse quant aux origines (géographiques et génétiques) des individus de Guyane et de Martinique, mais également sur les schémas de dispersion des individus subadultes entre leurs zones de développement et les zones d'alimentation et/ou de reproduction des adultes, durant une phase encore relativement méconnue de leur cycle de vie. Toutefois, un grand mystère plane encore sur la période précédant leur arrivée sur les habitats de développement, connue sous le nom de paradigme des "Années perdues" (Carr, 1987).

7.2.2 Les premières années de vie des émergences : les "Années perdues"

Comme nous l'avons vu en introduction (Chapitre 1), les jeunes tortues transitent d'abord pendant plusieurs années en plein océan avant de rejoindre leurs habitats de développement. Cette période est méconnue et les informations disponibles sont rares en raison de la petite taille des individus et de la difficulté de les capturer en plein océan (Mansfield *et al.*, 2014). Deux hypothèses majeures ont été évoquées concernant le déplacement de ces émergences, qui selon certains auteurs seraient uniquement entraînées passivement par les courants (théorie de la dispersion passive), et pour d'autres, nageraient au contraire activement malgré leur petite taille (théorie de la dispersion active).

Théorie de la dispersion passive

Du fait de leur petite taille durant les premières années de leur vie, on a longtemps pensé que les jeunes tortues (émergences) sont incapables de nager activement face aux puissants courants marins. Dans les années 1980, l'observation de jeunes tortues caouannes de Floride associées à des radeaux de Sargasses dérivants ont alimenté cette hypothèse de dérive passive (Carr & Meylan, 1980; Carr, 1986). Une dizaine d'années plus tard, l'émergence de modèles de circulation océanique a permis de simuler les déplacements passifs de jeunes tortues caouannes au départ de la Floride pour estimer le temps nécessaire pour traverser l'Atlantique nord avec la seule action des courants marins (Hays & Marsh, 1997). Depuis, plusieurs approches se sont attachées à simuler la distribution spatio-temporelle de ces émergences via :

- L'utilisation de bouées dérivantes lâchées depuis les sites de ponte des individus, *i.e. drifter* (Hays *et al.*, 2010; Blumenthal *et al.*, 2009; Mansfield & Putman, 2013; Monzón-Argüello *et al.*, 2010; Proietti *et al.*, 2012) ;
- Ou l'association de modèles de circulation océanique avec des modèles de simula-

tion de lâcher de particules inertes (Ascani *et al.*, 2016; Hays *et al.*, 2010; Hamann *et al.*, 2011; Gaspar *et al.*, 2012; Putman & Naro-Maciel, 2013; Putman *et al.*, 2013; Okuyama *et al.*, 2011).

Dans le Pacifique, Gaspar *et al.* (2012) ont notamment révélé que les eaux productives visitées par les simulations d'émergences de tortues luths coïncident avec les zones d'alimentation utilisées par les adultes de cette même espèce. Les auteurs ont donc fait l'hypothèse que les émergences mémorisent la position des zones d'alimentation rencontrées, pour y retourner une fois adultes. Il s'agit dans ce cas de la théorie du "but migratoire acquis" (*learned migration goal*, Gaspar *et al.* 2012; Scott *et al.* 2014). Toutefois, nous avons montré au cours de cette thèse que les tortues vertes adultes de Guyane réalisent une migration à contre-courant pour aller s'alimenter au large du Brésil. Pour valider l'hypothèse du bt migratoire acquis et donc, découvrir ces habitats d'alimentation au stade juvénile, cela suppose que les émergences de Guyane doivent traverser tout l'Atlantique nord via le gyre subtropical nord, puis revenir par le courant équatorial, pour enfin rejoindre les eaux brésiliennes. Or, les simulations réalisées par CLS (Toulouse) ont montré que même après 10 années passées en mer, les émergences nées en Guyane ne pourraient pas rejoindre les habitats d'alimentation du Brésil par la seule action des courants marins (Figure 7.5), ce qui remet en question l'hypothèse du but migratoire acquis et la théorie de la dérive exclusivement passive.

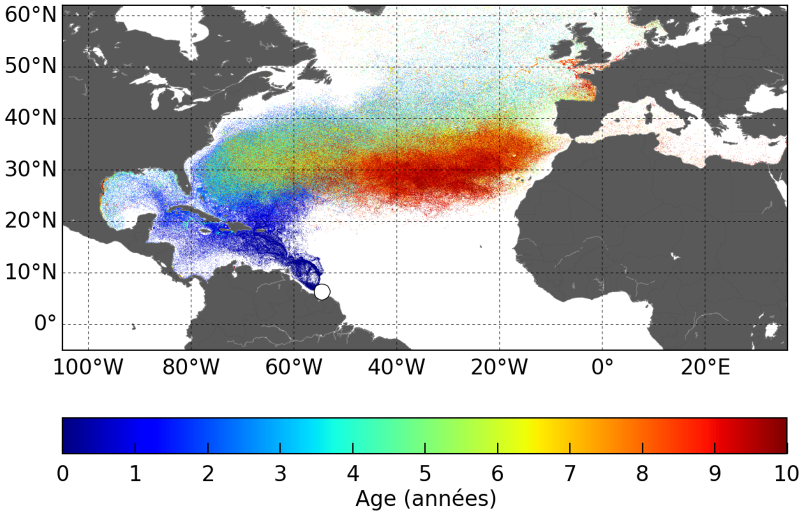


FIGURE 7.5 – Simulation de dérive passive d'émergences de tortues vertes au départ d'Awala-Yalimapo en Guyane française (carte réalisée par M. Lalire, CLS).

De plus, si l'on souhaite simuler la dispersion à plus long terme (> 6 ans) pour englober l'intégralité de la phase précédent le recrutement des individus (avant leur arrivée sur le site de développement, Chapitre 1), se pose alors la pertinence de l'hypothèse de dérive passive (Gaspar *et al.*, 2012). Au fur et à mesure de leur croissance, les individus augmentent leur capacité natatoire, et s'affranchissent par conséquent des courants marins. De récents modèles de dispersion ont ainsi intégré l'effet de la nage sur la dispersion des jeunes tortues, via la théorie de la dispersion active.

Théorie de la dispersion active

Ces six dernières années, un certain nombre d'études ont mis en évidence l'effet de la nage active dans la dispersion des émergences (Briscoe *et al.*, 2016; Gaspar *et al.*, 2012; Scott *et al.*, 2012b,a; Putman *et al.*, 2012a,b; Hamann *et al.*, 2011; Putman *et al.*, 2014, 2016). L'action conjuguée des courants marins et de la nage orientée des individus a ainsi pu être simulée grâce à l'ajout d'une direction (d'un cap) à la fin de chaque jour de simulation (Gaspar *et al.*, 2012; Scott *et al.*, 2012b,a), ou d'une vitesse de nage orientée au fur et à mesure que l'individu se déplace (Putman *et al.*, 2012a,b; Putman & Naro-Maciel, 2013; Hamann *et al.*, 2011; Putman *et al.*, 2014). Le suivi satellitaire de jeunes tortues caouannes dans l'Atlantique nord-ouest (âgées de 3,5 à 9 mois) a permis de soutenir l'hypothèse d'une dispersion active (Mansfield *et al.*, 2014). En effet, ces jeunes individus suivis n'ont pas été uniquement entraînés par le courant du gyre Atlantique subtropical nord (Carr, 1987; Witherington, 2002; Witherington *et al.*, 2012; Luschi *et al.*, 2003a; Bolten, 2003), mais au contraire ont, au moins pour certains, dévié leur trajectoire en quittant le gyre. Les travaux de Putman *et al.* (2014) ont également permis d'apporter un nouvel éclairage sur les "Années perdues" en combinant analyses génétiques et modèles de dispersion active, à partir de données issues de jeunes tortues imbriquées observées sur l'habitat d'alimentation de l'île de l'Ascension. L'analyse de marqueurs génétiques indique que ces individus sont majoritairement originaires de la côte sud-américaine (86%), et seulement 14% proviennent de la côte africaine. Ces résultats vont ainsi à l'encontre des simulations de dispersion uniquement passive, qui suggèrent une origine à l'est (côte africaine) et non à l'ouest (côte brésilienne). Afin d'étudier ce paradoxe, les auteurs ont réalisé une série de simulations (à rebours, en fixant plusieurs caps et vitesses différents), pour examiner le rôle de la nage orientée dans le transport des jeunes tortues imbriquées (Figure 7.6).

En assignant un cap à chaque position simulée, ce modèle de nage active a permis aux émergences simulées de rejoindre l'île de l'Ascension, mais aussi de se développer dans des eaux productives et thermiquement favorables (Putman *et al.*, 2014). De plus, l'âge des individus lors de leur arrivée à Ascension (4,5-5,5 ans) correspond à celui estimé à partir des données morphométriques des individus observés sur l'île, ce qui soutient l'hypothèse d'une stratégie de navigation orientée utilisée par les jeunes tortues marines.

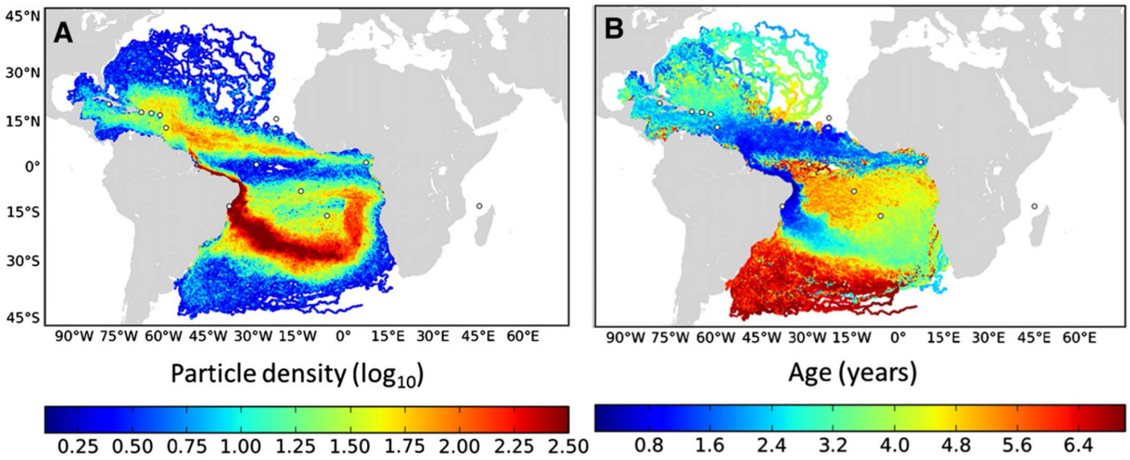


FIGURE 7.6 – Cartes issues des simulations (sur 7 ans) de dérive active d'émergences de tortues imbriquées au départ du nord-est du Brésil (5,67 °S, 36,8 °O, issu de Putman *et al.* 2014). (A) Densité d'individus dans chaque pixel et (B) âge moyen des individus dans chaque pixel.

Cette stratégie favorise ainsi leur croissance, augmente leur taux de survie et facilite leur migration transocéanique (Putman *et al.*, 2012a; Scott *et al.*, 2012b). Plus récemment, la comparaison entre les trajectoires réelles de tortues caouannes (29,7-37,5 cm) et les trajectoires simulées par dispersion passive (sous l'action des courants) ont montré des différences significatives, renforçant ainsi l'hypothèse d'une dispersion active dans les déplacements des émergences (Briscoe *et al.*, 2016). Une stratégie de navigation similaire a été observée chez d'autres espèces comme le saumon du Pacifique (Burke *et al.*, 2013), le homard (Boles & Lohmann, 2003), le triton (Phillips *et al.*, 2002) ou encore certaines espèces d'oiseaux (Beck & Wiltschko, 1998). Compte tenu des résultats obtenus à partir du suivi satellitaire des tortues vertes de Martinique et de Guyane française, il reste désormais à expliquer comment les tortues vertes de Guyane ont découvert leurs aires d'alimentation situées au large du Brésil. Est-ce un comportement inné ou bien acquis durant les premières années de vie ?

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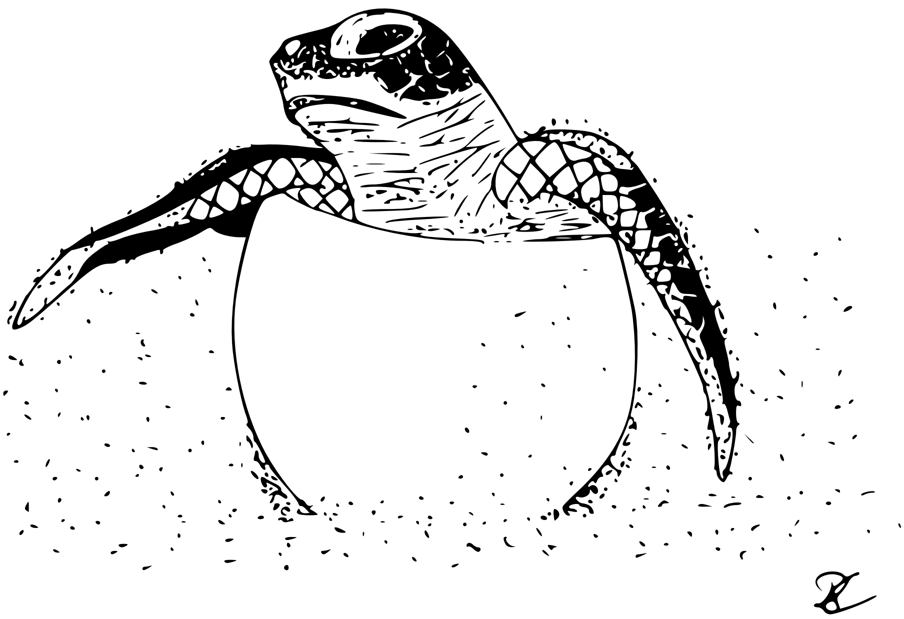
ANNEXE A

Inter-nesting behavioral adjustments of green turtles to an estuarine habitat in French Guiana

P. Chambault, B. de Thoisy, L. Kelle, R. Berzins, M. Bonola, H. Delvaux, Y. Le Maho, D. Chevallier. 2016. Inter-nesting behavioral adjustments of green turtles to an estuarine habitat in French Guiana. Marine Ecology Progress Series. 555. 235-248. 10.3354/meps11813.



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Inter-nesting behavioural adjustments of green turtles to an estuarine habitat in French Guiana

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ABSTRACT: Sea turtles adjust their behaviour according to the conditions of their habitat, thus saving or gaining energy during the energetically costly inter-nesting season. This study aimed to investigate how gravid green turtles *Chelonia mydas* nesting in Suriname and French Guiana have adapted to the unusual habitat of the Maroni River estuary, which has highly turbid and low salinity waters and *a priori* lacks seagrass, one of the main foods consumed by this species. Satellite telemetry was used to assess the behavioural adjustments of 26 adult females in terms of (1) home range and (2) diving behaviour, by recording the movements (location, dive depth, dive duration, surface duration) and environmental conditions (temperature and salinity of the water) experienced by each individual. The turtles exhibited limited movements, occupying a core home range of 512.7 km^2 and remaining close to the shore (3.8 ± 3.1 km) and the nesting beach (18.6 ± 22.7 km). Dive data showed that individuals spent extended periods at the surface (210 ± 288 min), probably associated with diurnal resting activity. The turtles performed uncharacteristically short and shallow dives (<5 min and <2 m) which could result from lung volume issues linked to positive buoyancy. This species shows a unique ability to tolerate extreme environments in this inter-nesting habitat, where large river outputs generate warm water (~27 to 29°C) and highly variable salinities (range: 1.2 to 35.5 psu). These results highlight the various behavioural adjustments of this population in response to the atypical and estuarine habitat of the Maroni river mouth.

KEY WORDS: *Chelonia mydas* · Guiana coast · Habitat use · Diving behaviour · Satellite tracking

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INTRODUCTION

To compensate for the high energy costs of reproduction, organisms must choose between 2 types of strategies: income breeding, whereby an animal feeds during reproduction, or capital breeding, whereby an animal stops feeding and relies solely on its body reserves (Drent & Daan 1980). Sea turtles are commonly considered as capital breeders, storing fat reserves at their foraging grounds then ceasing to feed during the breeding–nesting season (Drent & Daan 1980, Goldberg et al. 2013, Perrault et al. 2014), which occurs every 1 to 4 yr (Miller 1997). During this breeding–nesting period, gravid females must meet the high energy costs incurred by multiple activities that occur during the breeding–nesting season; i.e. migrating from the foraging grounds, mating, travelling to and from the nesting beach, incubating the clutch (50 to 150 eggs), laying eggs several times per season depending on the species (Miller 1997, Wal-

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lace et al. 2005, Walcott et al. 2012), and migrating back to the foraging areas — all potentially without feeding during at least 2 consecutive months (Schofield et al. 2013, Hays et al. 2014).

To limit the continuous loss of energy during the inter-nesting season, sea turtles have developed multiple strategies to maximize their reproductive output. For example, females have been reported to commonly rest on the seabed during U-shaped dives, as observed in green (Hays et al. 2000), hawksbill (Houghton et al. 2008, Walcott et al. 2013), loggerhead (Sakamoto et al. 1993, Houghton et al. 2002), and leatherback turtles (Reina et al. 2005). 'Assisted resting' has also been reported in Caribbean hawksbill turtles, which wedge themselves under coral reefs on the seafloor substrate during the inter-nesting season. Alternatively, gravid females can rest in mid-waters by controlling their lung volume to achieve neutral buoyancy, thereby limiting their energy expenditure (Minamikawa et al. 1997, Hays et al. 2000). In addition to diving adjustments, female sea turtles can restrict their movements by remaining close to the nesting beach (Stoneburner 1982, Hays et al. 1999, Blanco et al. 2013, Maxwell et al. 2014, Esteban et al. 2015). During the inter-nesting period, females can also show a preference for locations where optimal water temperatures enhance egg development prior to laying (Schofield et al. 2009, Fossette et al. 2012).

While some sea turtle populations have developed strategies to conserve energy during the inter-nesting season, others use specific behaviours to increase their energy reserves. Depending on local habitat conditions and the availability of food resources, gravid females can feed during the inter-nesting season (Hays et al. 2002c, Schofield et al. 2006, Georges et al. 2007). This behaviour has been highlighted for the green turtle in Cyprus (Hays et al. 2002c), where individuals perform shallower dives to forage on a site with seagrass beds, but has not been observed in females nesting in Ascension Island, where the apparent absence of a food supply prevents females from feeding during the inter-nesting season. Strong behavioural plasticity occurs in the case of habitat loss, when some individuals from the same population travel long distances to reach alternative breeding–nesting sites, whilst others remain close to the nesting beach, as recorded in loggerhead (Schofield et al. 2010a), hawksbill (Esteban et al. 2015), olive ridley (Hamel et al. 2008), leatherback (Shillinger et al. 2010) and green turtles (Troëng et al. 2005).

The dispersal and diving behaviour of gravid green turtles has been widely studied in many different nesting sites and shows strong inter-individual and inter-population variability, but to date, no information is available for the population nesting in the Suriname–French Guiana rookery. This site hosts one of the largest green turtle rookeries on the north-eastern part of the South American coast (Schulz 1975, Chevalier et al. 1998, Baudouin et al. 2015, Chambault et al. 2015), with 869 females and 2228 clutches counted in 2015 in French Guiana (Mast et al. 2016). The waters of the Guianese continental shelf contain large amounts of sediments and suspended materials continuously discharged by the Amazon River (Milliman & Meade 1983, DeMaster et al. 1996), leading to low levels of irradiance (Molleri et al. 2010) and presumably limiting the development of seagrass, one of the main foods consumed by adult green turtles. It is important to mention that although it is widely acknowledged that green turtles consume seagrass, there is no evidence to date of this occurring in Surinamese green turtles; Bjorndal (1982) suggests that they may feed on macroalgae. Located on both sides of the border between Suriname and French Guiana, this rookery is also influenced by the Maroni and the Mana rivers. Their mean discharge rates of 1680 vs. 300 $m^3 s^{-1}$, respectively (Lambs et al. 2007), make the water highly turbid and brackish (Jounneau & Pujos 1988) and bring high volumes of freshwater to the coast, especially during the rainy season (Lambs et al. 2007). This creates unusual estuarine conditions for sea turtles.

This study aims to investigate how gravid green turtles nesting in Suriname and French Guiana have adapted to the biological conditions of this estuarine habitat during the inter-nesting season. Satellite telemetry was used to assess the behavioural adjustments of 26 adult females in terms of home range and diving behaviour, by recording the movements and environmental conditions (temperature and salinity of the water) experienced by each individual. This is the first study to track this specific population of green turtles during the inter-nesting season in an unusual habitat influenced by large rivers, i.e. the Amazon, the Maroni and the Mana rivers.

MATERIALS AND METHODS

Ethics statements

This study meets the legal requirements of the countries where it was carried out, and follows all institutional guidelines. The protocol was approved by the Conseil National de la Protection de la Nature

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(CNPN; www.conservation-nature.fr/acteurs2.php?id=11), a branch of the French Ministry for Ecology, Sustainable Development and Energy acting as an ethics committee in French Guiana and Suriname (permit number: 09/618). After the evaluation of the project by the CNPN, fieldwork was carried out in strict accordance with the recommendations of the Police Prefecture of French Guiana (Cayenne, France), in order to minimize disturbance to the animals.

Satellite tag deployment

During the inter-nesting season, 16 Argos-linked Fastloc GPS tags (MK10, Wildlife Computers) were deployed on adult female green turtles from February to June 2012 on both sides of the Maroni River: at Awala-Yalimapo in the Amana Nature Reserve, French Guiana (5.7° N, 53.9° W, n = 8), and in the Galibi Nature Reserve in Suriname (5.4° N, 53.5° W, n = 8; see Fig. 1). During the same period in 2014, 10 additional females in the Amana Nature Reserve were equipped with Conductivity-Temperature-Depth-Fluorometer Satellite Relayed Data Loggers (CTD-SRDL; the Sea Mammal Research Institute Instrumentation). The attachment procedure followed the standard methods described in Baudouin et al. (2015). During tag deployment, measurements of the curved carapace length (CCL) were taken, and body mass was then calculated using the method of Hays et al. (2002a). A Platform Terminal Transmitter (PTT) was assigned to each turtle equiped with a tag.

Data collection

Inter-nesting route data were extracted following the procedure described by Baudouin et al. (2015). The Argos-linked Fastloc GPS tags recorded Argos locations and GPS positions of the turtles at 4 h intervals (10% of the locations transmitted). These tags also provided diving data, i.e. maximum dive depths, dive durations and *in situ* temperature data, binned as 4 h period histograms. Maximum depths were collected in different bins, every 10 m from 10 to 100 m, then every 50 m from 100 to 250 m. Maximum dive durations were stored from 30 s to 1 min, then every minute from 1 to 5 min, every 5 min from 5 to 20 min, and finally every 10 min from 20 to 60 min. *In situ* temperatures were recorded during dives from 20 to 32°C, every 1°C.

The CTD-SRDL tags provided the locations of the turtles via Argos data, and recorded simplified profiles of the diving parameters (dive depth, time at depth, dive duration and post-dive surface interval), and oceanographic data in the form of vertical temperature and salinity profiles taken during the ascent phase of the turtles' dives (Boehme et al. 2009). The CTD-SRDL tags were programmed to send summarized dive profiles using the compression algorithm described by Fedak et al. (2001), providing 4 depth records for each dive (instead of the single maximum depth per dive provided by Argos-Fastloc GPS tags). Temperature and salinity data were quality controlled using the procedure described in Roquet et al. (2011), with an estimated accuracy of 0.02°C and 0.05 psu.

Data pre-filtering

The tags were deployed at the beginning of the inter-nesting season, and therefore recorded location data for post-nesting migration. Following the procedure described in Baudouin et al. (2015), a spatial query was performed via ArcGIS version 10.1 (ESRI) to identify the date of migration departure. Only positions corresponding to the inter-nesting season were retained for analysis, as indicated in Chambault et al. (2015).

Using the same approach as Heerah et al. (2013), a Kalman-filtering algorithm was then applied (CLS; Collecte Localisation Satellites) to enhance tag position estimates (Argos and GPS) by accounting for Argos location errors (Patterson et al. 2010, Lopez et al. 2014). The General Bathymetric Chart of the Oceans database (GEBCO, www.gebco.net/; 30 arc-second 1 km grid) was used to discard any locations on land. Positions associated with a speed of >5 km h^{-1} (Hays et al. 2004, Schofield et al. 2013) and those with location Class Z (class associated with the raw location before Kalman filtering) were considered insufficiently accurate and were removed.

Data analyses

The 'trackDistance' function from the 'trip' package in R (Luque 2007) was used to calculate distance travelled and elapsed time between locations. Observed speed was then derived from these values. Distance to shore was calculated by finding the shortest distance to the coastline for each turtle location, using the 'dist2Line' function from the 'geosphere' package (Robert 2015). Distance to nesting site, i.e. the location where each turtle was initially tagged, was also calculated for each position.

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All statistical analyses were performed using R software version 3.2.2 (R Core Team 2014). Before being submitted to statistical tests, all samples were checked for normality (Shapiro-Wilk test) and homogeneity of variance (Levene's test). The results of these tests determined the subsequent use of either parametric or nonparametric tests for sample analysis, with a significance level of $\alpha = 0.05$. Values are means ± SD.

For the diving variables, we discriminated between benthic and pelagic dives by calculating the difference between the bathymetry at the dive location and the maximum dive depth recorded by the CTD-SRDL for the same location for each dive. Dives with a maximum depth within 1 m of the seabed were classified as benthic dives, and those with a maximum depth beyond 1 m of the seabed were pelagic dives. Data from the Argos-linked Fastloc GPS tags (n = 16) were not used due to their coarser resolution (1 dive depth every 10 m). At some locations, depth difference was greater than the bathymetry depth, possibly due to the error generated by the shift between the incorrect Argos positions and the considerable movements of the turtle during the dive.

To obtain an idea of the dive patterns, we calculated the Time of Allocation at Depth (TAD) index by using the 4 inflection points of the summarized profiles provided by the CTD-SRDL tags. Based on the method of Fedak et al. (2001), TAD calculation makes it possible to obtain relevant information about where turtles concentrate their activity within the dives, i.e. V-shaped dives for $0.5 \leq \text{TAD} < 0.75$ (exploratory dives) and U-shaped dives for $0.75 \leq \text{TAD} < 1$ (activity centered at the bottom of the dive, linked to either foraging or resting activity). Following the method of Plot et al. (2015), the average rate of change of depth was fixed at 1.4 m s^{-1}. Bottom time was calculated as the time spent below 80% of the maximum depth (Heerah et al. 2013), and the descent and ascent rates (in m s^{-1}) were also determined. The day hours were set from 06:00 to 18:00 h local time to assess potential diel dive patterns.

Home range estimation

In order to display residency patterns, both the Argos and GPS positions were used to estimate home ranges by mapping kernel density distributions (Worton 1989). Although GPS locations are more accurate than Argos locations for the quantification of home ranges (Schofield et al. 2010b), the low number of GPS locations transmitted (10%) made it impossible to base the kernel calculation on GPS data alone. To minimize autocorrelation in spatial analyses, median daily locations were generated for each turtle (Schofield et al. 2010b, 2013, Revuelta et al. 2015). A kernel density analysis was then carried out for each year of tag deployment using the 'kernelUD' function from the 'adehabitatHR' package in R (Calenge 2006). As kernel density cannot always be calculated using the least square cross-validation method (Seaman & Powell 1998), the smoothing parameter was set using the default approach, i.e. the ad hoc method (Calenge 2006). Ninety percent density contours were used to represent the broad home range, and 50% density contours were used to indicate the core area. The corresponding area (expressed in km^2) was then calculated within each kernel contour.

Nesting events and basking identification

Nesting events were identified using direct observation during nocturnal surveys rather than evidence of haul-outs from tracking data. This choice is explained by the lack of precise resolution from the Argos (>1500 m) and GPS locations (<100 m) and the potential inaccuracy of the GEBCO database in such coastal habitat, making the identification of nesting events unreliable if based on tracking data alone. Daily nocturnal patrols were therefore performed from February to July during each year of tag deployment (2012 and 2014) on Awala-Yalimapo beach (Amana Nature Reserve) to observe the entire nesting season of green turtles in this rookery. Each observed female was scanned to identify a Passive Integrated Transponder (PIT). If the individual was not tagged, a PIT was inserted in the top right triceps muscle. The GPS location of the animal, time, PIT number, beach location (sand, bank, vegetation or water) and behaviour (rise, first sweep, digging, second sweep, laying, filling or U-turn) were systematically recorded for each individual throughout the nesting periods. To avoid any possibility of false nesting events affecting the results, only laying behaviour was retained for analysis.

The haul-out information recorded by the wet/dry sensor of the tags was also used to identify surface resting/basking behaviour. The Fastloc-GPS tag sensor enters haul-out state after 20 consecutive dry minutes, and exits haul-out state if it remains wet for 30 s or more. For CTD-SRDL tags, a haul-out was recorded when the saltwater switch dry time exceeded 10 min, and the end of the haul-out was

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registered after a submersion time of at least 40 s. Any haul-outs that were recorded during the daytime were considered as Extended Surface Times (ESTs; Hochscheid et al. 2010), the latter being considered as evidence of surfacing/resting behaviour, as green turtles nest exclusively by night on this site (D. Chevallier unpubl. data).

RESULTS

Capture-mark-recapture data

A total of 475 female green turtles were observed nesting at Awala-Yalimapo beach (French Guiana) from 30 January to 12 July 2012; 669 were observed during the same period in 2014. The average inter-nesting interval between 2 consecutive clutches was 12.8 ± 1 d in 2012 (n = 2329) and 12.6 ± 1.4 d in 2014 (n = 2160). The activity peak occurred in April of both years, with 2329 nesting events recorded in 2012 and 2160 in 2014. Nocturnal patrols recorded an average 2.4 ± 1.6 nesting events per turtle during the tracking period (range: 1 to 5; Table 1).

General tracking data

The inter-nesting data recorded from the tags covered the period from February to July in 2012 and 2014. The tag instruments transmitted for an inter-nesting tracking duration ranging from 4 d (#115458) to 95 d (#130766; see Table S1 in the Supplement at www.int-res.com/articles/suppl/m555p235_supp.pdf) for an average of 254 ± 144 locations (5.4 ± 1.7 locations d^{-1}). Only 1 of the 16 turtles equipped during the inter-nesting season in 2012 (#115459) did not transmit any location data during the inter-nesting season. The CCL of these green turtles varied from 103 to 133 cm (mean: 115.5 ± 5.8 cm; #130776 vs. #130773) and their body mass ranged from 130.8 to 238.1 kg (mean: 177 ± 16.5 kg; #130776 vs. #130773).

Displacement and home range

Total distance travelled varied from 28 km (#115458) to 2627 km (#130766; Table 1). Gravid green turtles travelled over longer distances in 2014

Table 1. Horizontal movements of the 25 gravid green turtles *Chelonia mydas* tracked in 2012 and 2014. PTT: turtle ID. Values are mean ± SD

PTT	Instrument	Nesting events	Distance (km)	Distance to shore (km)	Distance to nest (km)	Speed (km h^{-1})
115445	MK10	3	928	6.9 ± 7.2	24 ± 29	1.6 ± 1.3
115446	MK10	1	1323	3.7 ± 2.8	8.1 ± 5.1	1.1 ± 1.1
115447	MK10	1	764	2.3 ± 2.0	8.4 ± 4.6	0.8 ± 0.9
115448	MK10	1	727	2.2 ± 1.7	7.6 ± 3.8	0.8 ± 0.9
115449	MK10	1	547	2.9 ± 2.4	14 ± 11	0.8 ± 0.9
115450	MK10	1	881	2.7 ± 2.2	11 ± 3.1	1.1 ± 1.1
115451	MK10	5	871	4.5 ± 4.7	14 ± 14	0.9 ± 1.1
115452	MK10	1	523	3.1 ± 4.2	11 ± 5.1	0.9 ± 1.1
115453	MK10	1	479	2.9 ± 2.1	9.9 ± 3.0	0.7 ± 0.8
115454	MK10	1	812	2.4 ± 2.0	8.6 ± 4.8	1.1 ± 1.1
115455	MK10	1	486	4.3 ± 3.0	13 ± 7.3	1.0 ± 1.0
115456	MK10	2	688	2.4 ± 2.3	14 ± 16	1.2 ± 1.1
115457	MK10	1	362	2.7 ± 1.8	5.9 ± 1.8	0.8 ± 0.9
115458	MK10	1	28	0.6 ± 0.5	2.8 ± 1.9	1.1 ± 0.9
115460	MK10	2	305	2.7 ± 2.2	7.8 ± 6.0	1.3 ± 1.1
130766	CTD-SRDL	4	2627	16.0 ± 26.0	96 ± 110	1.5 ± 1.2
130767	CTD-SRDL	5	533	1.6 ± 2.0	5.2 ± 8.3	0.9 ± 1.0
130768	CTD-SRDL	5	849	1.5 ± 1.6	12 ± 11	0.9 ± 0.9
130769	CTD-SRDL	5	570	5.1 ± 5.4	18 ± 17	1.0 ± 1.0
130770	CTD-SRDL	2	345	3.0 ± 2.6	6.0 ± 3.9	0.9 ± 1.1
130771	CTD-SRDL	4	671	5.3 ± 3.8	18 ± 16	1.2 ± 1.1
130773	CTD-SRDL	5	535	2.5 ± 2.4	6.6 ± 4.9	0.9 ± 0.9
130776	CTD-SRDL	2	680	2.9 ± 2.6	84 ± 56	1.5 ± 1.4
131354	CTD-SRDL	4	1578	8.8 ± 18	35 ± 59	1.4 ± 1.3
131355	CTD-SRDL	1	286	3.8 ± 4.4	26 ± 18	1.0 ± 0.9
		2.4 ± 1.6	736 ± 510	3.8 ± 3.1	18.6 ± 22.7	1.1 ± 0.2

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(867.4 ± 714.6 km) than the females tracked in 2012 (648.2 ± 310.6 km). In 2014, 2 individuals (#130766 and #131354) performed large loops towards the French Guianese and the Brazilian coasts, whereas the 8 other turtles mostly remained close to the shoreline during the inter-nesting season (Fig. 1). The distance to shore ranged from 0.6 ± 0.5 km (#115458) to 16 ± 26 km (#130766), with turtles remaining on average within 3.8 ± 3.1 km from the coastline (Fig. 1, Table 1). The green turtles remained within 18.6 ± 22.7 km of the nesting site (range: 2.8 to 96 km; #115458 vs. #130766, respectively). The average travel speed was 1.1 ± 0.2 km h^{-1} (range: 0.7 to 1.6 km h^{-1}; #115453 vs. #115445, respectively; Table 1).

A daily average of 5.5 ± 3.6 locations was retained to perform the kernel analysis. There was clear inter-annual variability in the habitat used by turtles: in 2012, the broad home range (90% kernel estimator) measured 351.3 km^2 and the core home range (50% kernel estimator) covered only 89.9 km^2 (Fig. 2A), whereas the 10 gravid females tracked in 2014 used a much broader home range (up to 42 times larger than in 2012) with a 90% kernel contour that covered 15 050 km^2, concentrating their activity within a 1620.8 km^2 area (Fig. 2B).

Diving behaviour

Data from Argos-Fastloc GPS tags

The 15 Argos-linked Fastloc GPS tags deployed in 2012 provided 5522 records of maximum dive depths and 5305 records of dive durations. Maximum dive depths differed significantly between individuals (Kruskal-Wallis rank sum test, $p < 0.001$), and varied from 0 to 150 m, with 80% of the dives performed in the upper 10 m (Fig. 3A). Dive durations differed significantly between individuals (Kruskal-Wallis rank sum test, $p < 0.001$) and ranged from 30 s to 70 min, with 35% of the dives lasting up to 5 min (Fig. 3B).

The number of ESTs recorded by the Argos-Fastloc GPS tags varied from 1 to 6 per individual (#115447,

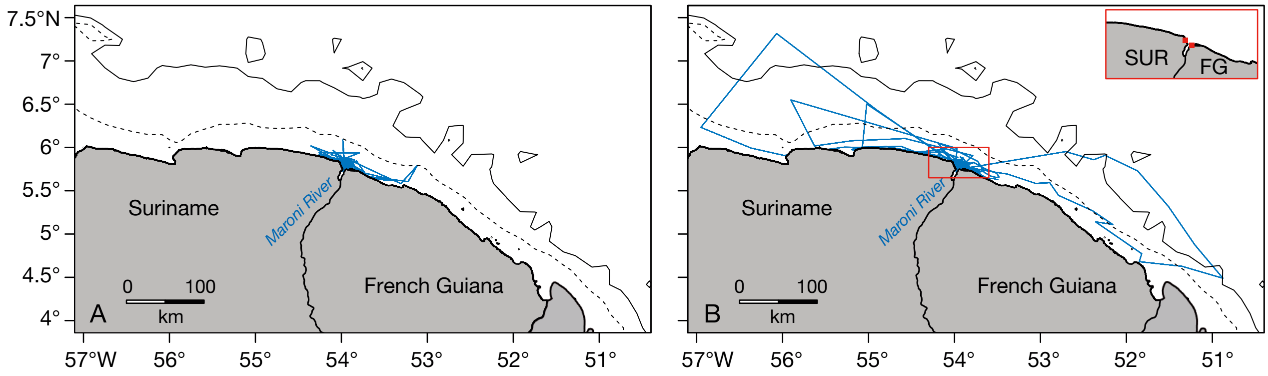

Fig. 1. Trajectories of the gravid green turtles *Chelonia mydas* tracked in (A) 2012 (n = 15) and (B) 2014 (n = 10). The 2 tagging sites are presented in the red rectangle in B (SUR = Suriname and FG = French Guiana)

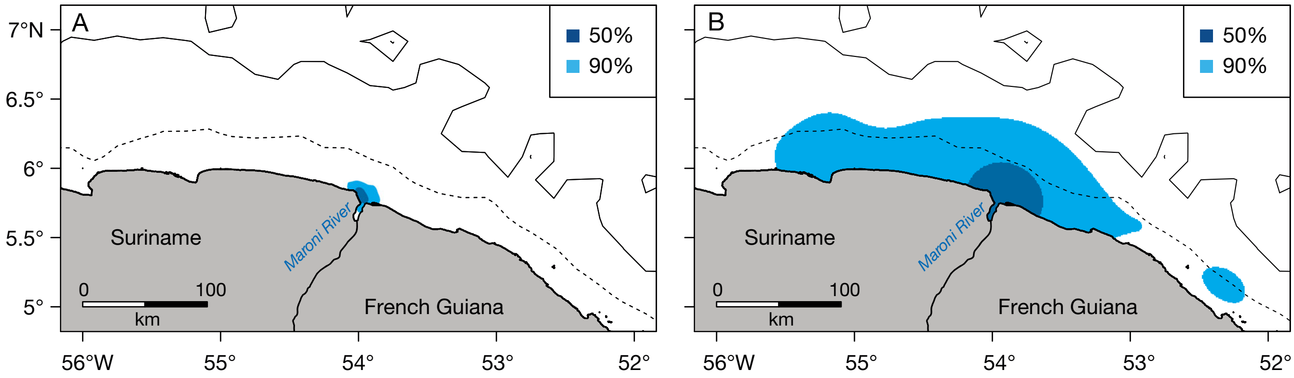

Fig. 2. Kernel density contours (90% in turquoise; 50% in dark blue) of (A) the 15 green turtles *Chelonia mydas* tracked in 2012 and (B) the 10 turtles tracked in 2014

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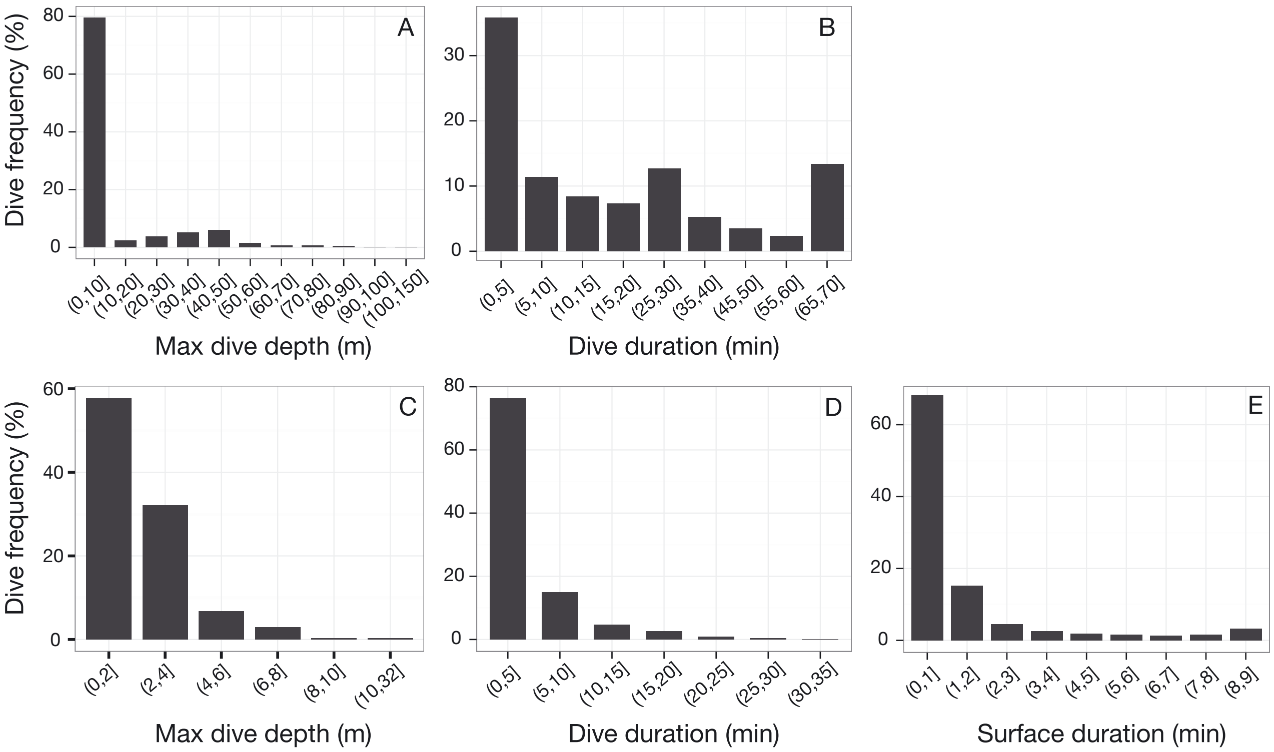

Fig. 3. Diving variables recorded by the (A,B) Argos-Fastloc GPS tags and (C–E) CTD-SRDL tags showing maximum dive depth (A,C), dive duration (B,D), and post-dive surface interval (E) for all individual green turtles *Chelonia mydas*. The bins differ from those described in the 'Materials and methods' section as they were combined for a better visual representation

#115452, #115457 vs. #115455), with an average of 1.7 ± 1.0 per female, and mostly occurred late in the afternoon, at 17:00 h. The possible inaccuracy of the bathymetry extracted in this coastal region (~1 km resolution) made it impossible to differentiate between terrestrial and surface basking. Unfortunately, the Argos-Fastloc GPS tags did not provide any information regarding EST duration.

Data from the CTD-SRDL tags

The 10 CTD-SRDL tags deployed in 2014 provided reliable data for 1237 summarized dive profiles. Average maximum dive depth was 2.6 ± 2.1 m, ranging from 1 to 32.5 m, and 59% of the dives were performed within the upper 2 m (Fig. 3C). Maximum dive depths were significantly different between individuals (Kruskal-Wallis rank sum test, $p < 0.001$). The maximum dive depth did not differ significantly between day and night (2.5 ± 1.5 vs. 2.8 ± 2.7 m; Mann-Whitney *U*-test, p = 0.5723).

Dive durations varied from 30 s to 35 min and lasted on average 4.0 ± 4.7 min, with 79% of the dives lasting <5 min (Fig. 3D). Dive durations differed significantly between individuals (Kruskal-Wallis rank sum test, $p < 0.001$). Dive duration was not significantly different between day and night (3.8 ± 4.7 vs. 4.2 ± 4.9 min; Mann-Whitney *U*-test, p = 0.4819).

Post-dive surface duration ranged from 0.06 s to 8.1 min, for an average duration of 1.3 ± 1.9 min. Seventy percent of the post-dive surface intervals lasted <1 min, and differed significantly between individuals (Kruskal-Wallis rank sum test, $p < 0.001$) (Fig. 3E). Surface duration did not differ significantly between day and night (1.33 ± 1.87 vs. 1.42 ± 2.02 min; Mann-Whitney *U*-test, p = 0.3993).

The average TAD was 0.71 ± 0.15, indicating mainly V-shaped dives. However, other dive shapes were also performed by the green turtles, as 43% of the dives were associated with a TAD ranging between $0.75 \leq \text{TAD} < 1$ (resting U-shaped dives), and 47% were associated with a TAD between $0.5 \leq \text{TAD} < 0.75$ (exploratory V-shaped dives). Bottom time lasted on average 2.5 ± 4.0 min, ranging from 0 to 34.1 min, meaning that the turtles spent 52.3% of the diving time at the bottom. Average descent rate was 0.21 ± 0.20 m s^{-1} while the average ascent rate was 0.03 ± 0.03 m s^{-1}. Of the 1237 summarized dives

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retained for the analysis, 62% were benthic dives and 38% were pelagic, showing a difference between bathymetry and maximum dive depth >1 m (Fig. 4).

The number of ESTs varied between 3 and 29 per individual (#131355 vs. #130767), with an average of 13.6 ± 9.5 per female during this period. EST duration ranged from 10 min (#130767 and #130771) to 1920 min (#131355), with an average duration of 210 ± 288 min.

Temperature and salinity data

During the 2012 inter-nesting season, the Argos-Fastloc GPS tags recorded 2169 temperature values ranging from 24 to 33°C, for an average temperature of 28.4 ± 1.1°C. Eighty-six percent of the dives were performed in warm waters with temperatures between 27 and 29°C (Fig. 5); there were also inter-individual differences in the mean temperature (Kruskal-Wallis rank sum test, $p < 0.001$). A slight increase was observed in water temperature throughout the tracking months, with the coolest values in April (mean: 28.2 ± 1.2°C) and the warmest in June (29.0 ± 0.9°C).

During the 2014 inter-nesting season, 57 of the CTD profiles analysed recorded a total of 516 temperature and salinity values. Salinity ranged from 1.2 to 35.5 psu (mean: 24.6 ± 10.3 psu), and temperatures varied from 25.3 to 28.4°C (26.8 ± 0.5°C) (Fig. 6). All turtles used a broad range of oceanographic structures, especially in terms of salinity (Fig. 6).

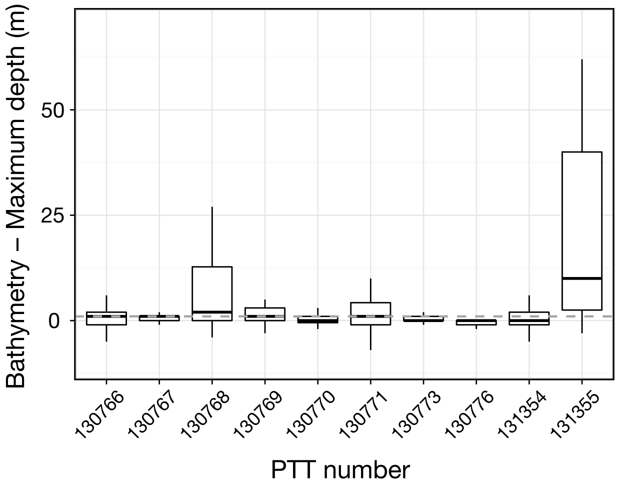

Fig. 4. Depth difference between bathymetry and maximum dive depth data from the 10 CTD-SRDL tags of each individual green turtle *Chelonia mydas* equipped in 2014. Dashed line: limit between benthic (depth difference ≤1 m) and pelagic dives (depth difference >1 m)

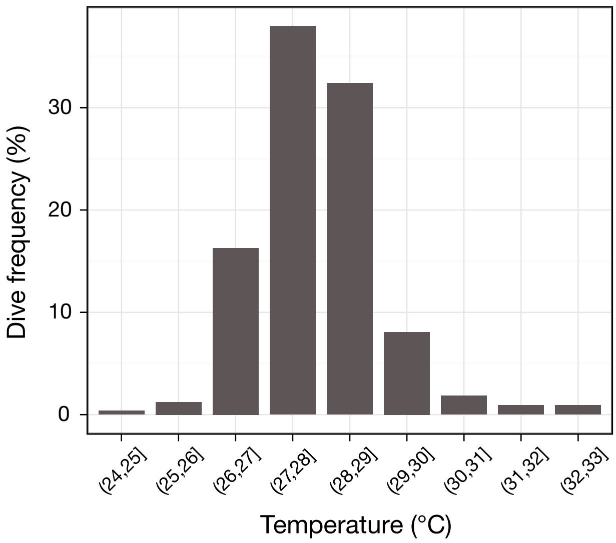

Fig. 5. *In situ* temperatures recorded by the 15 Argos-linked Fastloc GPS tags deployed on green turtles *Chelonia mydas* in 2012

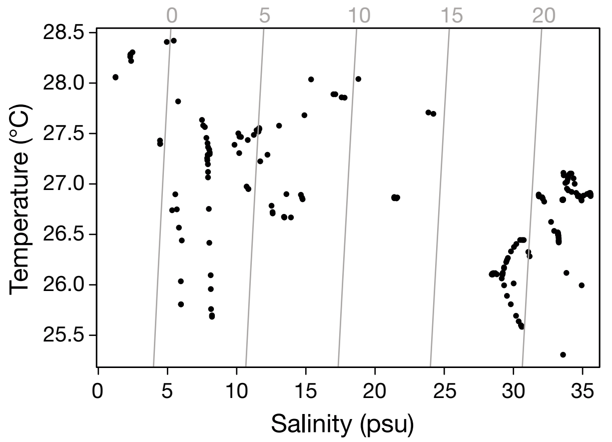

Fig. 6. Temperature–salinity diagram for the 10 individual green turtles *Chelonia mydas* fitted with a CTD-SRDL tag in 2014. Grey lines and numbers: isopycnal lines and values

DISCUSSION

This tracking of green turtles from Suriname and French Guiana during the inter-nesting season provides the first data to describe their inter-nesting events, habitat use, dispersal and diving behaviour. These results highlight the various behavioural adjustments of this population in response to the atypical and estuarine habitat of the Maroni river mouth.

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Inter-nesting events

Direct observation (nocturnal patrols) showed the inter-nesting interval to be 12.8 ± 1 d in 2012 (n = 2329) and 12.6 ± 1.4 d in 2014 (n = 2160) (range: 5 to 18 d), which is within the range recorded for other green turtle populations in the Atlantic (range: 10 to 14 d; Carr et al. 1974, Hays et al. 2002b), Caribbean (9 to 13 d; Bjorndal & Carr 1989, Esteban et al. 2015), and Pacific (10 to 15 d; Blanco et al. 2013). Because the turtles were equipped with transmitters on both sides of the Maroni river mouth, we can be certain that they were nesting on both the Surinamese and French Guianese beaches. However, the number of nesting events per female may be underestimated as the nocturnal patrols were only performed on the beaches of French Guiana, which may explain the long inter-nesting interval for some individuals. Simultaneous direct observation of individuals on both sides of the river mouth therefore appears to be a crucial source of additional information for tracking data, and annual monitoring on the Surinamese side is also necessary in order to paint a clear picture of the inter-nesting period.

Habitat use

Despite the high inter-annual variability of the habitat, kernel analysis indicated that the turtles spent most of their time in a relatively small area measuring 512.7 km^2 (50% contour). Although this core range was significantly larger than the 50% contour for East Pacific green turtles (3 km^2; Blanco et al. 2013), the French Guiana turtles concentrated their activity close to the nesting beach (range: 2.8 to 96 km, mean: 18.6 ± 22.7 km). This mirrors habitat use by green turtles in Florida (6 to 11 km; Hart et al. 2013). Gravid green turtles may therefore reduce the energy costs of locomotion by limiting their movements, as their home range is dictated by their metabolic rate (Slavenko et al. 2016).

Our estimation of home range should, however, be interpreted with caution, as the kernel densities were obtained from both Argos and GPS data. In some cases, the estimated Argos position can be some km away from the true location (Rutz & Hays 2009). This explains the high number of locations on land (32%) that had to be discarded from the analysis. The use of Argos-Fastloc GPS tags made it possible to increase the accuracy of the location estimations, which is crucial when dealing with resident animals whose movements occur on a very small scale. Argos locations had to be included in the kernel analysis, as the unique surfacing behaviour of green turtles (brief and slanting) resulted in the transmission of a very low number (7%) of GPS locations. The low number of GPS positions could also be explained by the GPS sampling interval, which was fixed to 4 h. Although a shorter sampling interval would have increased the number of GPS locations recorded, it would have also reduced the lifespan of the tag. This would have been counterproductive, as our objective was to record both the inter-nesting and migration periods for each tracked individual.

The associated habitat was characterized by low salinity and highly turbid waters resulting from the large river outputs that are continuously discharged onto the Guiana continental shelf (Jounneau & Pujos 1988, Froidefond et al. 2002). Close to the Maroni and Mana rivers, the Kaw estuary, located 250 km southeast of the rookery, has a wide range of salinities (range: 0.1 to 19 psu) that vary according to the combined effect of rainfall (2000 to 4000 mm yr^{-1}; Lambs et al. 2007) and tides (Jounneau & Pujos 1988, Lam-Hoai et al. 2006). Négrel & Lachassagne (2000) reported that the salinity of the Kaw estuary dropped to 0.1 psu during the rainy season (April to July), similar to the salinity values recorded by tags on the turtles in our study. The green turtles were tracked from the beginning of the long rainy season (April to June), and the resulting data confirms that they crossed highly contrasted ecosystems in terms of salinity, varying from oligohaline (<5 psu) to ultrahaline habitats (>35 psu). Such results are consistent with the highly variable water properties recorded in the Maroni estuary (salinity range: 0 to 20 psu) due to the high rainfall (mean: 2000 to 2500 mm; data from Météo-France) and the flow of the river during this period (mean discharge: 1680 m^3 s^{-1}; Jounneau & Pujos 1988, Artigas et al. 2003). *Chelonia mydas* therefore shows a high tolerance to a wide range of environments in French Guiana, as observed in the loggerhead turtle in southwest Florida (salinity range: 0 to 40 psu; Foley et al. 2006) and the Kemp's ridley turtle in the Gulf of Mexico (Metz 2004).

The water temperatures experienced by tracked green turtles (mean: 26 to 28°C) were similar to those recorded by the olive ridley sea turtles tracked over the Guiana shield (26.2 to 27.8°C; Plot et al. 2012). The temperature range appeared to be slightly wider for the green turtles (range: 23 to 33°C) than that recorded by their conspecifics from the Atlantic (range: 27 to 28°C; Hays et al. 2002b) and Pacific oceans (range: 27 to 29°C; Blanco et al. 2013). The higher temperatures observed in French Guiana

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could be explained by the warmer freshwater of the Maroni and Mana rivers (Nikiema et al. 2007), especially during the period of maximum river discharges from May to June (Artigas et al. 2003). Indeed, the highest temperatures recorded in 2012 (29 to 33°C) were mostly located at the mouth of the river, close to the Surinamese nesting beach. Furthermore, the high temperature values recorded in our study are consistent with the samples taken by Négrel & Lachassagne (2000) in the Maroni estuary (range: 23.8 to 33.4°C).

Distance to shore

All 25 females tracked in this study remained close to the shore throughout the inter-nesting season, i.e. within 3.8 ± 3.1 km of the coastline. Similar patterns were observed in green turtles nesting in Tortuguero, Costa Rica, which stayed within 30 km of the coastline (Troëng et al. 2005). The females tracked in the present study remained essentially close to their rookery (20.5 ± 44.4 km), showing strong nest-site fidelity. This has been highlighted for green turtles in the Atlantic (Hart et al. 2013) and Pacific oceans (Blanco et al. 2013). By remaining close to their nesting site, gravid green turtles are probably saving energy for oviposition. However, some inter-individual differences were observed (range: 2.8 to 96 km), particularly for one turtle that travelled over 368 km from the nesting beach (#130766). Similar extensive movements during the inter-nesting season have been recorded in loggerhead turtles in the Mediterranean Sea (Schofield et al. 2010b), as some females may leave the vicinity of the rookery without necessarily nesting on alternative sites. In contrast, some females do show a lack of nest-site fidelity and nest on alternative sites, as observed in green and hawksbill turtles from the Lesser Antilles in the Caribbean (Esteban et al. 2015). The associated travel speeds of the turtles tracked in our study (1.1 ± 0.2 km h^{-1}, range: 0.7 to 1.6 km h^{-1}) were close to those reported by Troëng et al. (2005) (mean: 0.9 ± 1.0 km h^{-1}) and to those recorded in the green turtle population of Ascension Island (mean: 1.5 km h^{-1}, range: 0.9 to 3.5 km h^{-1}; Carr et al. 1974).

Diving behaviour

The dives performed in 2014 by the green turtles during the inter-nesting season were shallow (59% of dives <2 m) and short (79% of dives <5 min). Similar behaviour has been observed in East Pacific green turtles tracked from Costa Rica (69% <5 m; 72% between 2 and 10 min; Blanco et al. 2013), and also in the leatherback population using the same Awala-Yalimapo nesting site in French Guiana (59% <5 m, 60% <6 min; Fossette et al. 2007). Such behaviour indicates that the gravid turtles studied are mainly influenced by the bathymetry of the inter-nesting habitat. The GEBCO database shows bathymetry to be below 5 m at the mouth of the Maroni River, where the turtles spend most of their time. The dive durations were much shorter than those recorded in Ascension Island green turtles, which mainly rested during the inter-nesting season (mean: 22.1 vs. 7.3 min while migrating; Hays et al. 1999). Additionally, green turtles must reach an optimal depth of 19 m to achieve negative buoyancy for resting after fully inflating their lungs at the surface (Hays et al. 2000). The short, shallow dives of the French Guianese green turtles in the very shallow habitat of the Maroni River mouth could therefore be linked to short-term resting activity caused by lung volume issues. Low visibility could also explain the very short duration of dives, causing turtles to return frequently to the surface to find their way using air-borne chemosensory cues (Endres & Lohmann 2013, Endres et al. 2016).

Alternatively, the short dives observed in French Guiana could be linked to foraging activity, as also observed in Australian green turtles (Hazel et al. 2009). However, the high river outputs lead to low levels of irradiance (Seminoff et al. 2002), probably resulting in a lack of seagrass in this inter-nesting habitat. If the turtles feed during the inter-nesting period, such conditions could encourage them to feed on other resources such as invertebrates, macroplankton or macroalgae (Bjorndal 1982). The foraging ecology of *Chelonia mydas* varies greatly among geographical regions (Buttemer & Dawson 1993, Heithaus et al. 2002, Hatase et al. 2006, Amorocho & Reina 2007, Burkholder et al. 2011, Blanco et al. 2013) and is particularly diverse in estuarine habitats, where this species has been observed to consume mainly animal matter, i.e. crustaceans, molluscs, polychaetes and cnidarians (González Carman et al. 2012, Santos et al. 2015). Jellyfish are also particularly abundant on the French Guiana continental shelf (Fossette et al. 2009), providing an alternative source of nutrition that may enable this green turtle population to adapt to the local conditions of this habitat. However, a visual investigation would be required to confirm this assumption, as was previously carried out on green and loggerhead turtles in the Mediterranean Sea (Hays et al. 2002b, Schofield et al. 2006). Other devices such as jaw sensors could

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also be used in future studies to investigate if green turtles feed during the inter-nesting season in French Guiana (Fossette et al. 2008).

Gravid green turtles are known to commonly alternate between different activities at sea during this period, i.e. travelling, resting or foraging (Cheng et al. 2013), and change between different dive shapes, i.e. U (resting/foraging dives), V (exploratory dives) or S (energy-saving swimming); see Hochscheid et al. (1999) for further information. This was reflected in our results, where 43% of the dives were U-shaped and 47% were V-shaped. To confirm the occurrence of these different activities, it would be necessary to deploy acceleration data loggers, as used by Cheng et al. (2013), and perform isotopic analyses, oesophageal lavages and gut content analysis to assess the types of prey consumed during the inter-nesting season (Hatase et al. 2006, Amorocho & Reina 2007).

Multiple extended surface intervals were identified by the tags, and may be associated with a resting activity for prolonged periods (mean: 210 ± 288 min). Unlike East Pacific green turtles, the daytime surfacing behaviour of the females tracked in our study suggests basking at the surface. Such behaviour can be beneficial for thermoregulation (Sapsford & van der Riet 1979, Hochscheid et al. 2010), avoidance of aggressive males or potential predators (Swimmer 2006), delay of algal or fungal infestations and even enhancement of immune response (Boyer 1965, Swimmer 2006). Although some visual investigation is needed, such extended periods of hauling out could be associated with terrestrial basking on a persistent sandbank located in the core area of the green turtles (D. Chevallier unpubl. data). Two tags recorded extremely long periods of hauling out (>1300 min, ~22 h). These unusual basking events were occasional, and could be caused by turtles becoming trapped in the mud, the shrubby vegetation, or the decomposing wood accumulated on the beach in piles that can be several meters high. This phenomenon was observed for one female (#131355) in 2014 (D. Chevallier unpubl. data). Indeed, the multiple mudbanks along the shores of French Guiana and Suriname (Allison & Lee 2004, Anthony et al. 2010, 2015, Péron et al. 2013), are generated by the sediment discharges from the Amazon River, and this dynamic ecosystem leads to continuous erosion and accretion processes. The basking behaviour described in this study may be related to resting activity and an uptake of solar radiation by individuals for thermoregulation (Whittow & Balazs 1982, Hochscheid et al. 2010, Van Houtan et al. 2015).

Conservation implications

Satellite tracking of the green turtle population nesting in Suriname and French Guiana made it possible to locate and quantify the habitat used by this species during the inter-nesting season. The survival of this endangered species is at risk given its limited dispersal close to its nesting beaches and the life-threatening risk of illegal fishing along the Guiana coast (Charuau 2002, DEAL Guyane 2013). An evaluation of their home range is essential to obtain a reliable picture of core activity areas and identify hotspots for the protection of this endangered species (Scott et al. 2012, Schofield et al. 2013, Pendoley et al. 2014). The high energetic costs of reproduction and nesting activities make the green turtle particularly vulnerable during the breeding–nesting period, especially in highly turbid waters such as those of the Maroni River, where visibility is significantly reduced (Metz 2004). Although there is some inter-annual variability, the limited core home ranges found in this study (i.e. the areas where turtles concentrate their activity) may facilitate the implementation of adequate measures on a regional scale. Such measures include recording the location of illegal fisheries by the National Navy, the French National Agency for Hunting and Wildlife (ONCFS) or the Amana Nature Reserve, thus enabling us to focus on conservation efforts in this critical habitat. Indeed, the home range estimation derived from this study closely overlaps with a major fishing ground unit (Levrel 2012, Chevallier 2013). We therefore recommend further study to evaluate the interactions between gravid green turtles and fisheries, and thus permit the delineation of a Marine Protected Area that would cover the core area of this endangered species. Given the nesting peak of this population (i.e. from April to June) and the location of its habitat (at the natural border between Suriname and French Guiana), an open dialogue is crucial if we hope to redefine international fishing practices and ensure the conservation of this endangered species.

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ANNEXE B

Habitat use and diving behaviour of gravid olive ridley sea turtles under riverine conditions in French Guiana

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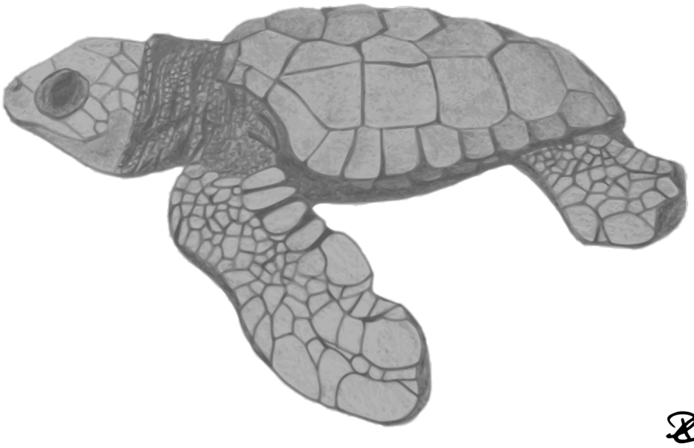

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Habitat use and diving behaviour of gravid olive ridley sea turtles under riverine conditions in French Guiana

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ABSTRACT

The identification of the inter-nesting habitat used by gravid sea turtles has become a crucial factor in their protection. Their aggregation in large groups of individuals during the inter-nesting period exposes them to increased threats to their survival - particularly along the French Guiana shield, where intense legal and illegal fisheries occur. Among the three sea turtle species nesting in French Guiana, the olive ridley appears to have the most generalist diet, showing strong behavioural plasticity according to the environment encountered. The large amounts of sediments that are continuously discharged by the Amazon River create a very unusual habitat for olive ridleys, i.e. turbid waters with low salinity. This study assesses the behavioural adjustments of 20 adult female olive ridleys under such riverine conditions. Individuals were tracked by satellite from Remire-Montjoly rookery in French Guiana using tags that recorded the location and diving parameters of individuals, as well as the immediate environment of the turtles including the in situ temperature and salinity. Data concerning potential preys was provided via collection of epifauna by a trawler. Multiple behavioural shifts were observed in both horizontal and vertical dimensions. During the first half of the inter-nesting season, the turtles moved away from the nesting beach (21.9 ± 24.7 km), performing deeper (12.6 ± 7.4 m) and longer (29.7 ± 21.0 min) dives than during the second half of the period (7.4 ± 7.8 km, 10.4 ± 4.9 m and 25.9 ± 19.3 min). Olive ridleys remained in waters that were warm (range: 26–33 °C) and which fluctuated in terms of salinity (range: 19.5–36.4 psu), in a relatively small estuarine habitat covering 423 km^2. If olive ridleys were foraging during this period, the potential preys that might be available were mostly crustaceans (43%) and fish (39%), as expected for the diet of this generalist species during this period. This study highlights the numerous behavioural adaptations of this species in response to the unusual riverine conditions of the French Guiana continental shelf.

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1. Introduction

The tracking of highly mobile organisms through satellite telemetry helps to identify key breeding and foraging areas that play a crucial role in species conservation (Stokes et al., 2015). Given the high inter-individual plasticity of these migrant organisms, long-term monitoring is usually required to delineate adequate protected areas based on species distribution (Schofield et al., 2010). A better understanding of how animals interact with their environment is therefore needed to implement efficient conservation measures, especially when dealing with threatened species such as sea turtles.

The use of satellite tracking to study sea turtles movements and their habitat use during the breeding-nesting season highlighted strong site fidelity for both males and females (Schofield et al., 2010; Hays et al., 2014; Chambault et al., 2016b). The identification of such habitat is of major importance due to the large aggregation of individuals close to the nesting beaches during this period. Additionally, such periods make sea turtles particularly vulnerable due to the high energy costs of the reproduction and the nesting activities. An evaluation of the home range is an essential tool to establish a picture of the core activity areas for the protection of such endangered species (Scott et al., 2012; Schofield et al., 2013; Pendoley et al., 2014). This tool has been widely used to support conservation initiatives for leatherback (Witt et al., 2008), kemp ridley (Seney and Landry, 2008), loggerhead (Schofield et al., 2010; Hart et al., 2010), green (Richardson et al., 2013; Hart et al., 2013; Blanco et al., 2013), hawksbill turtles (Marcovaldi et al., 2012; Hart et al., 2012; Revuelta et al., 2015) and olive ridleys (Maxwell et al., 2011).

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During the inter-nesting season, olive ridley sea turtles show a strong behavioural plasticity in their dispersal and diving behaviour (Hamel et al., 2008; Maxwell et al., 2011; Pikesley et al., 2013). According to the geographic area and therefore the resources available, olive ridleys can adopt either a capital breeding strategy, in which they store fat reserves at their foraging grounds and then cease to feed during the breeding-nesting season (Drent and Daan, 1980), or use an income breeding strategy, whereby they continue to feed throughout the reproduction period (Miller, 1997; Colman et al., 2014).

The olive ridley is distributed across all tropical and subtropical waters, and appears to be the most abundant sea turtle species (Godfrey and Godley, 2008). This species has been studied in the Pacific (Polovina et al., 2004; Swimmer et al., 2006, 2009; Plotkin, 2010), the Arafura Sea off Northern Australia (Whiting et al., 2007; McMahon et al., 2007; Hamel et al., 2008; Pikesley et al., 2013), and in the Indian (Rees et al., 2012) and Atlantic Oceans (Reis et al., 2010; Maxwell et al., 2011). In the western part of the Equatorial Atlantic, French Guiana hosts one of the largest population of olive ridleys (Kelle et al., 2009; The State of the World's Sea Turtles, 2016). This olive ridley population has already been tracked during post-nesting migration (Plot et al., 2015; Chambault et al., 2016a), but only one study to date has focused on the movements and diving behaviour of this species during the inter-nesting season, highlighting the surprising reproductive synchrony of olive ridleys nesting in French Guiana (Plot et al., 2012).

The Guianese continental shelf is strongly enriched by the large amounts of sediments and suspended materials that are continuously discharged by the Amazon River (Milliman and Meade, 1983; DeMaster et al., 1996), creating turbid and warm waters that fluctuate drastically in terms of salinity between the dry and the rainy season. Given the active behaviour adopted by this population during the post-nesting migration (Chambault et al., 2016a) and the inter-nesting season (Plot et al., 2012), and in view of the abundance of potential prey for olive ridleys over the French Guiana shield (Guéguen, 2000), we hypothesize that gravid females nesting in French Guiana will dive consistently, adjusting their behaviour to the fluctuating conditions encountered on the Guianese continental shelf.

To assess olive ridley behavioural shifts in response to estuarine conditions, twenty adult females were equipped with satellite tags on Remire-Montjoly beaches (French Guiana) in 2013 and 2014. The tags recorded the behaviour (location and diving parameters) of animals and sampled the in situ temperature and salinity of their immediate environment. Combined with the details of available prey collected in trawl nets, the information supplied by these tags will help to characterize (1) the displacements and (2) the diving behaviour of this vulnerable species in this unusual habitat during the energetically costly inter-nesting season.

2. Methods

2.1. Ethics statements

This study meets the legal requirements of the countries where this work was carried out, and follows all institutional guidelines. The protocol was approved by the “Conseil National de la Protection de la Nature” (CNPN, http://www.conservation-nature.fr/acteurs2.php?id=11), the French Ministry for Ecology, Sustainable Development and Energy (permit Number: 09/618) acting as an ethics committee in French Guiana. After the evaluation of the project by the CNPN, fieldwork was carried out in strict accordance with the recommendations of the Police Prefecture of French Guiana, Cayenne, France, in order to minimize the disturbance of animals.

2.2. Study site and animal tagging

During the inter-nesting seasons in 2013 and 2014, 20 adult female olive ridleys were fitted with satellite tags on Remire-Montjoly beaches (4.53°N, −52.16°W, Cayenne, French Guiana). From 26/06/13 to 29/06/13, 8 Argos-linked Fastloc GPS tags (MK10, Wildlife Computers Redmond, WA, USA) and 2 Conductivity Temperature Depth Fluorometer-Satellite Relayed Data Loggers (CTD-SRDL, Sea Mammal Research Unit, University of St. Andrews, Scotland) were deployed. From 25/06/14 and 30/07/2014, 10 additional CTD-SRDL tags were fitted on olive ridleys. The attachment procedure followed the standard methods described in Baudouin et al. (2015).

2.3. Data collection

2.3.1. Nocturnal patrols

Nesting events were identified using direct observation during nocturnal surveys rather than evidence of haul-outs from tracking data. This choice is explained by the lack of precise resolution from the Argos (>1500 m) and GPS locations (<100 m) and the potential inaccuracy of the GEBCO database in such coastal habitat, making the identification of nesting events unreliable if based on tracking data alone. Daily nocturnal patrols were therefore performed from April to September in 2013 and 2014 on Remire-Montjoly and Cayenne beaches to observe the entire nesting season of olive ridley turtles. Using the same procedure as that described in Chambault et al. (2016a), each observed female was scanned with a TROVAN Reader to identify a Passive Integrated Transponder (PIT) and if the individual was not tagged, a PIT was inserted in the top right triceps muscle. To complete these nocturnal patrols, daily counts of female's traces on the beach were conducted each day to ensure that no nesting event was missed.

2.3.2. Argos-linked Fastloc GPS tags

The procedure to extract the inter-nesting route data was identical to that used in Baudouin et al. (2015). The Argos-linked Fastloc GPS tags recorded Argos locations and GPS positions at 4-hour intervals (<1% of the locations transmitted). These tags also provided diving data, i.e. maximum dive depths, dive durations and in situ temperature data, binned as 4-hour period histograms. Maximum depths were collected in different bins, every 10 m from 10 to 100 m, then every 50 m from 100 to 250 m. Maximum dive durations were stored from 30 s to 1 min, then every minute from 1 to 5 min, and finally every 10 min from 10 to 60 min. In situ temperatures were recorded during dives from 20 to 32 °C, every one degree Celsius.

2.3.3. CTD-SRDL tags

The CTD-SRDL tags provided the locations of animals via Argos data and recorded simplified profiles of the diving parameters (dive depth, time at depth, dive duration and post-dive surface interval) and oceanographic data in the form of vertical temperature and salinity profiles taken during the ascent phase of turtle dives (Boehme et al., 2009). The CTD-SRDL tags were programmed to send summarized dive profiles using the compression algorithm described by Fedak et al. (2001), providing four depth records for each dive (instead of the single maximum depth per dive provided by Argos-linked Fastloc GPS tags). Temperature and salinity data were quality controlled using the procedure described in Roquet et al. (2011), with an estimated accuracy of 0.02 °C in temperature and 0.05 psu in salinity.

2.3.4. Prey abundance from trawler

Over the French Guiana continental shelf, 31 samples of potential olive ridley prey (epifauna) were collected during a survey carried out by IFREMER using a bottom trawler between 15/11 and 20/11/2014. The fauna was sampled with a shrimp trawl (1 m vertical opening, 6.7 m horizontal opening, 45 mm cod-end mesh size). The trawl hauls were performed on the seafloor at depths of 10 to 60 m. All the individuals collected at each location were identified and counted. As it was not possible to identify the specific species of some individuals, we classified the preys into five groups: cephalopods, crustaceans, cnidarians, molluscs and osteichthyes (fishes).

2.4. Data pre-filtering

As the tags were deployed at the beginning of the inter-nesting season, they also recorded locations from the post-nesting migration. Following the procedure described in Chambault et al. (2015), the average daily speed during the inter-nesting season was calculated, a speed filter of 30 km.d^{-1} was set, and only the positions associated with a daily speed >30 km.d^{-1} were set to migration phase and then excluded for the analysis. Following the same procedure as Chambault et al. (2015), only the positions corresponding to the inter-nesting season were retained for the analysis.

Using the same approach as Heerah et al. (2013), a Kalman-filtering algorithm was then applied (*CLS, Collecte Localisation Satellites*, Toulouse, France) to enhance tag position estimates by accounting for Argos location errors (Patterson et al., 2010; Lopez et al., 2014). The General Bathymetric Chart of the Oceans database (GEBCO, http://www.gebco.net/, 30-arc-second 1 km grid) was used to discard any locations on land (13% and 10% of the locations recorded in 2013 and 2014, respectively). Positions associated with a speed of over 5 km.h^{-1} (2% in 2013 and 2% in 2014) (Hays et al., 2004; Schofield et al., 2013) and those with location class Z (class associated with the raw location before Kalman filtering, 1 location recorded in 2013) were considered insufficiently accurate and were removed.

The *trackDistance* function from the *trip* package on R (Luque, 2007) was used to calculate the distance travelled and the elapsed time between locations. The observed speed was then derived from these values. The distance to the nesting site, i.e. the location where each turtle was initially tagged, was also calculated for each position.

2.5. Habitat use

In order to display the residency patterns, both the Argos and GPS positions were used to estimate the home ranges by mapping the kernel density distributions (Worton, 1989). Although GPS locations are much more accurate than Argos locations for the quantification of home ranges (Schofield et al., 2010), we could not base the kernel calculation only on GPS data due to the very low amount of GPS locations transmitted (1%). To minimize autocorrelation in spatial analyses, median daily locations were generated for each turtle (Schofield et al., 2010, 2013; Revuelta et al., 2015). Based on the coordinates expressed in decimal degree (limiting possible errors given the proximity to the equator), a kernel density analysis was then designed combining both years of tag deployment using the *kernelUD* function from *adehabitatHR* package on R (Calenge, 2006). As the kernel density cannot always be calculated using the least square cross-validation method (Seaman and Powell, 1998), the smoothing parameter *h* was fixed using the default approach, i.e. the ad hoc method with $h = 0.08$ (Calenge, 2006). Ninety percent contours were used to represent the broad home range, and 50% density contours were used to define the core area. The corresponding area (expressed in km^2) was then calculated within each kernel contour.

2.6. Diving behaviour

For the diving variables, we discriminated between benthic and pelagic dives by calculating the difference between the bathymetry at the dive location and the maximum dive depth recorded by the CTD-SRDL for the same location for each dive. Therefore, dives with a maximum depth within 0 m of the seabed were classified as benthic dives, and those with a maximum depth above 0 m of the seabed were pelagic dives. Data from the Argos-linked Fastloc GPS tags ($n = 8$) were not used due to their coarser resolution (one dive depth every 10 m). At some locations, depth difference was greater than the bathymetry depth, possibly due to the error generated by the shift between the incorrect Argos positions and the considerable movements of the turtle during the dive or due to GEBCO errors in such coastal habitats.

To obtain an idea of the dive patterns, we calculated the Time of Allocation at Depth (TAD) index by using the four inflection points of the summarized profiles provided by the CTD-SRDL tags. Based on Fedak et al. (2001)'s method, TAD calculation makes it possible to obtain relevant information about where turtles concentrate their activity within the dives, i.e. V-shaped dives for $0.5 \leq \text{TAD} < 0.75$ (exploratory dives) and U-shaped dives for $0.75 \leq \text{TAD} < 1$ (activity centered at the bottom of the dive, linked to either foraging or resting activity). Following the method of Plot et al. (2015), the average rate of change of depth was fixed at 1.4 m.s^{-1}.

2.7. Statistical analyses

All statistical analyses were performed using R software version 3.2.2 (R Core Team, 2015). Before being submitted to statistical tests, all samples were checked for normality and homogeneity of variance by means of the Shapiro-Wilk test. Depending on these results, parametric or nonparametric tests were used, with a significance level of $\alpha = 0.05$. Values are means ± SD.

3. Results

3.1. Horizontal movements

3.1.1. Capture-mark-recapture data

During the period from April to September, a total of 1644 gravid female olive ridleys were observed nesting in Remire-Montjoly and Cayenne beaches in 2013 and 1125 gravid females in 2014. The activity peak occurred in July of both years, with 859 nesting events recorded in 2013 and 654 in 2014. Nocturnal patrols recorded an average 1.1 ± 0.3 and 1.2 ± 0.4 nesting events per turtle in 2013 and 2014, respectively (range: 1–4).

3.1.2. General tracking data

Among the ten females equipped in 2013, two individuals (#131354 and #131355) started their post-nesting migration directly after the tag deployment, and were therefore discarded from the analyses. In 2014, four turtles (#130765, #136775, #136776 and #136778) were also removed from the analyses due to very short tracking duration (3, 1, 8 and 4 days, respectively). The data for the horizontal movements of the 14 remaining turtles are summarized in Table 1. On average, 212 ± 93 locations were recorded per tag, for an average tracking duration ranging from 23 (#130767 and #130769) to 54 days (#130765a and #136773, Table 1).

The total distance travelled varied from 342 km (#136772) to 1101 km (#130771), for an average distance of 592 ± 237 km (Table 1). The average travel speed was 1.1 ± 0.1 km.h^{-1} (range: 0.8 ± 0.8 km.h^{-1} #136772 vs. 1.4 ± 1.1 km.h^{-1} #130771). The distance travelled differed significantly among individuals in 2013 (Kruskal-Wallis rank sum test: $\chi^2 = 34$, df = 7, $p < 0.001$), and in 2014 (Kruskal-Wallis rank sum test: $\chi^2 = 14$, df = 5, $p < 0.05$). In 2013, the daily speed ranged from 16.9 ± 9.6 km.d^{-1} (#136770) to 24.4 ± 11.3 km.d^{-1} (#130771), for an average daily speed of 20.1 ± 10.8 km.d^{-1}. In 2014, the daily speed ranged from 16.6 ± 9.9 km.d^{-1} (#136779) to 23.8 ± 21.8 km.d^{-1} (#130776), for an average daily speed of 17.2 ± 10.5 km.d^{-1}. Similarly, the daily speeds also differed significantly among individuals in 2013 but not in 2014 (2013: Kruskal Wallis rank sum test, $\chi^2 = 15$, df = 7, $p < 0.05$; 2014: $\chi^2 = 2.3$, df = 5, $p = 0.79925$, respectively).

3.1.3. Distance to the nesting beach

The distance to the nesting beach varied over the inter-nesting period. Although the turtles moved farther away in 2013 compared to 2014 (up to 38 km vs. 20 km, Figs. 1 and 2A), the same pattern was observed for both years: a sharp increase was observed in the distance to the nesting site during the first half of the tracking (2013: 24.3 ± 25.9 km

Table 1
Summary of the horizontal movements of the olive ridleys equipped in 2013 and 2014. PTT refers to the turtle ID, and Nloc to the number of locations recorded.

PTT	Instrument	Start date	Migration start	Nloc	Tracking duration (d)	Distance travelled (km)	Speed (km.h^{-1})
130764a	MK10	27/06/13	22/07/13	178	25	371	1.1 ± 0.9
130765a	MK10	26/06/13	19/08/13	445	54	939	1.1 ± 1.0
130766	MK10	27/06/13	06/08/13	277	40	778	1.2 ± 1.1
130767	MK10	28/06/13	21/07/13	159	23	346	0.9 ± 1.1
130768	MK10	27/06/13	03/08/13	239	37	726	1.3 ± 0.9
130769	MK10	27/06/13	20/07/13	102	23	390	1.3 ± 1.1
130770	MK10	28/06/13	04/08/13	259	37	528	1.1 ± 1.0
130771	MK10	27/06/13	08/08/13	334	42	1101	1,4 ± 1.1
130764	CTD-SRDL	29/07/14	27/08/14	190	29	529	1.1 ± 1.0
136772	CTD-SRDL	25/07/14	20/08/14	115	26	342	0.8 ± 0.8
136773	CTD-SRDL	29/07/14	21/09/14	205	54	803	1.1 ± 1.0
136774	CTD-SRDL	30/07/14	28/08/14	139	29	449	1.3 ± 1.3
136777	CTD-SRDL	30/07/14	28/08/14	178	29	514	1.0 ± 0.9
136779	CTD-SRDL	25/07/14	29/08/14	150	35	484	0.9 ± 0.9
				212 ± 93	35 ± 10.3	592 ± 237	1.1 ± 0.1

vs. 2014: 24.2 ± 25.5 km), followed by a decrease with turtles remaining within 10 km of the nesting beach (Fig. 1). During the second phase of the nesting season, the turtles remained an average 7.4 ± 8.0 km from the beach in 2013, and up to 7.4 ± 7.9 km in 2014. However, the distance to the nesting beach varied among individuals for each year (2013: Kruskal-Wallis rank sum test, $\chi^2 = 115$, df = 7, $p < 0.001$; 2014: Kruskal-Wallis rank sum test, $\chi^2 = 46$, df = 5, $p < 0.001$).

3.1.4. Home range

There was a slight inter-annual variability regarding the core home range (50% kernel estimator) used by the turtles as it covered 434 km^2 in 2013, compared to 398 km^2 in 2014. The broad home range (90% kernel estimator) was twice higher in 2013 (3257 km²) compare to 2014 (1587 km^2). The total home range for both years of tag deployment extended over 2916 km^2, and the turtles centered their activity (50% kernel contours) within a 423 km^2 area (Fig. 2B).

3.2. Vertical movements

3.2.1. Maximum depth, dive duration and surface interval

Among the 20 tags deployed in 2013 ($n = 10$) and 2014 ($n = 10$), 14 were retained for the diving behaviour analyses, with the Argos-linked Fastloc GPS tags providing 4904 depth records and 4788 dive durations, and the CTD-SRDL tags recording 696 dives.

3.2.1.1. Argos-linked Fastloc GPS tags. In 2013, the maximum dive depth differed significantly between individuals (Kruskal-Wallis rank sum test: $\chi^2 = 316$, df = 7, $p < 0.001$), and ranged from 0 to 50 m (mean: 12.6 ± 6.7 m), with 82% of the dives performed in the upper 10 m (Fig. 3A). Dive durations differed significantly between individuals (Kruskal-Wallis rank sum test: $\chi^2 = 206$, df = 7, $p < 0.001$) and ranged from 0 to 70 min (mean: 30.6 ± 19.8 min), with 44% of the dives lasting up to 20 min (Fig. 3B).

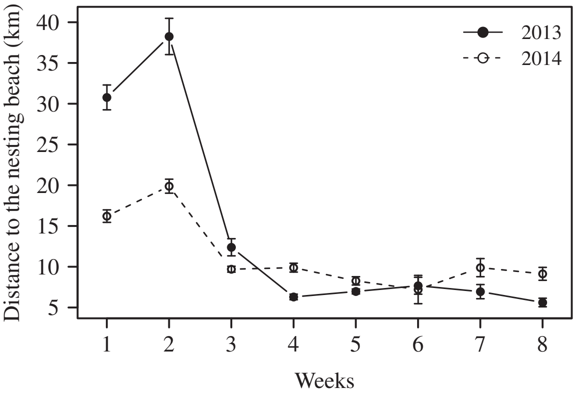

Fig. 1. Distance to the nesting beach in 2013 (filled dots) and 2014 (open dots) over the weeks during the inter-nesting season.

3.2.1.2. CTD-SRDL tags. In 2014, the maximum dive depth differed significantly between individuals (Kruskal-Wallis rank sum test: $\chi^2 = 28$, df = 5, $p < 0.001$), and ranged from 0 to 35 m (mean: 5.6 ± 4.4 m), with 90% of the dives performed in the upper 10 m (Fig. 3C).

Dive durations differed significantly between individuals (Kruskal-Wallis rank sum test: $\chi^2 = 16$, df = 5, $p < 0.005$) and ranged from 0 to 95 min (mean: 8.6 ± 12.4 min), with 77% of the dives lasting up to 10 min (Fig. 3D).

Post-dive surface interval ranged from 0.06 s to 9 min, for an average duration of 1.0 ± 0.9 min. Eighty-eight percent of the post-dive surface intervals lasted <2 min, and differed significantly between individuals (Kruskal-Wallis rank sum test: $\chi^2 = 35$, df = 5, $p < 0.001$, Fig. 3E).

3.2.2. Dive shape

Eighty-three percent of the dives performed by the turtles tracked in 2014 were benthic dives, and 16% were pelagic dives. The average TAD was 0.76 ± 0.14, indicating mainly U-shaped dives. Fifty-nine percent of the dives were associated with a TAD ranging between $0.75 \leq \text{TAD} < 0.1$ (resting U-shaped dives), and 37% were associated with a TAD between $0.5 \leq \text{TAD} < 0.75$ (exploratory V-shaped dives).

V-shaped dives were predominant at the beginning of the tracking period, then decreased until the week 5 and then increased again (Fig. 4). Inversely, the U-shaped benthic dives increased over the period, i.e. from week 1 to week 5, and then decreased again. The U-shaped pelagic dives were the less abundant type of dives.

3.2.3. Diving behavioural shifts over the inter-nesting season

The diving behaviour varied over the inter-nesting season. Although the turtles dived deeper and for longer durations in 2013 compared to 2014 (up to 17.8 m vs. 7.8 m; up to 44.1 min vs. 13.1 min), the same pattern was observed for both years but less pronounced in 2014, with deeper and longer dives during the first three weeks of tracking for both years, followed by shallower and shorter dives for the rest of the inter-nesting season (Fig. 5A and B). The post-dive surface interval recorded in 2014 followed the same pattern (Fig. 5C).

3.2.4. Habitat characterization

3.2.4.1. Potential preys collected from the trawler. The data for prey sampled by the trawler (IFREMER French Guiana) between 15/11 and 20/11/2014 provided 31 records from depths of 12–51.8 m along the French Guiana coast. During the sampling period, a total of 8730 organisms belonging to five different groups were collected: crustaceans ($n = 4489$), osteichthyes (fish, $n = 3063$), molluscs ($n = 976$),

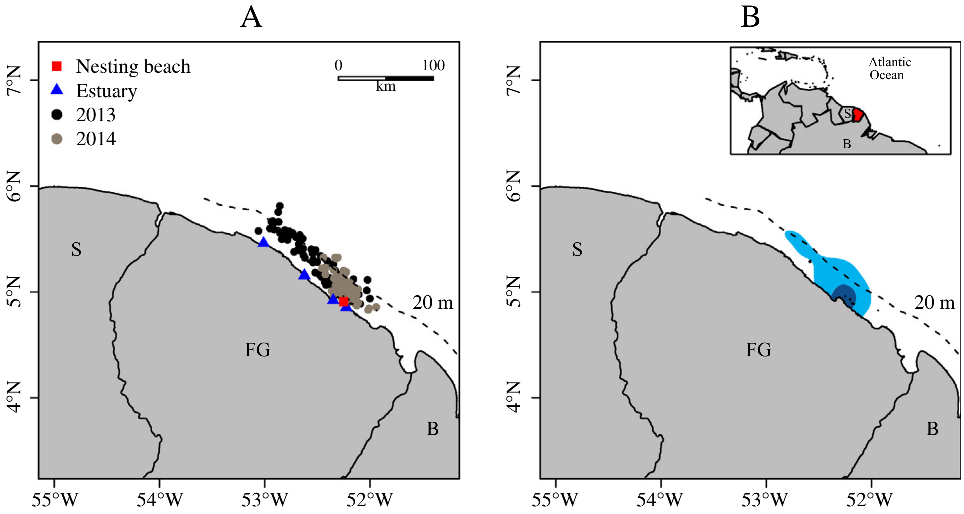

Fig. 2. (A) Median daily locations of the 14 olive ridleys tracked in 2013 (black dots) and 2014 (grey dots) and (B) kernel contours (90% shown in turquoise and 50% shown in dark blue) of the 14 olive ridleys tracked in 2013 and 2014. French Guiana is highlighted in red in B. FG stands for French Guiana, S for Suriname and B for Brazil. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

cephalopods ($n = 162$) and cnidarians ($n = 17$). Over the 31 samplings, the crustacean group was the most abundant, representing 51% of the samples, followed by the osteichthye group (35%). Seven samples were collected within the 90% kernel contour of 2014 (Fig. 3A), and mainly contained two highly abundant groups: crustaceans (43%) and osteichthyes (39%) – see Fig. 6B.

3.2.4.2. Oceanographic data recorded by the tags. In 2013, the Argos-linked Fastloc GPS tags recorded 1224 temperature values, ranging from 26 to 33 °C, for an average temperature of 28.3 ± 1 °C (Fig. 7A). Seventy-six percent of the dives were performed in warm waters with temperatures between 27 and 29 °C.

In 2014, the CTD-SRDL tags recorded 91 temperature values, ranging from 26.1 and 28.1 °C (mean: 26.7 ± 0.4 °C), and 84 salinity values, ranging from 19.5 to 36.4 psu (mean: 32.8 ± 5 psu) – see Fig. 7B. All turtles had used a broad range of oceanographic structures, crossing three different density patches.

4. Discussion

The tracking of these 20 gravid olive ridleys over the French Guiana continental shelf provides crucial information about (i) their habitat use and (ii) behavioural shifts that occur during the energetically costly inter-nesting season.

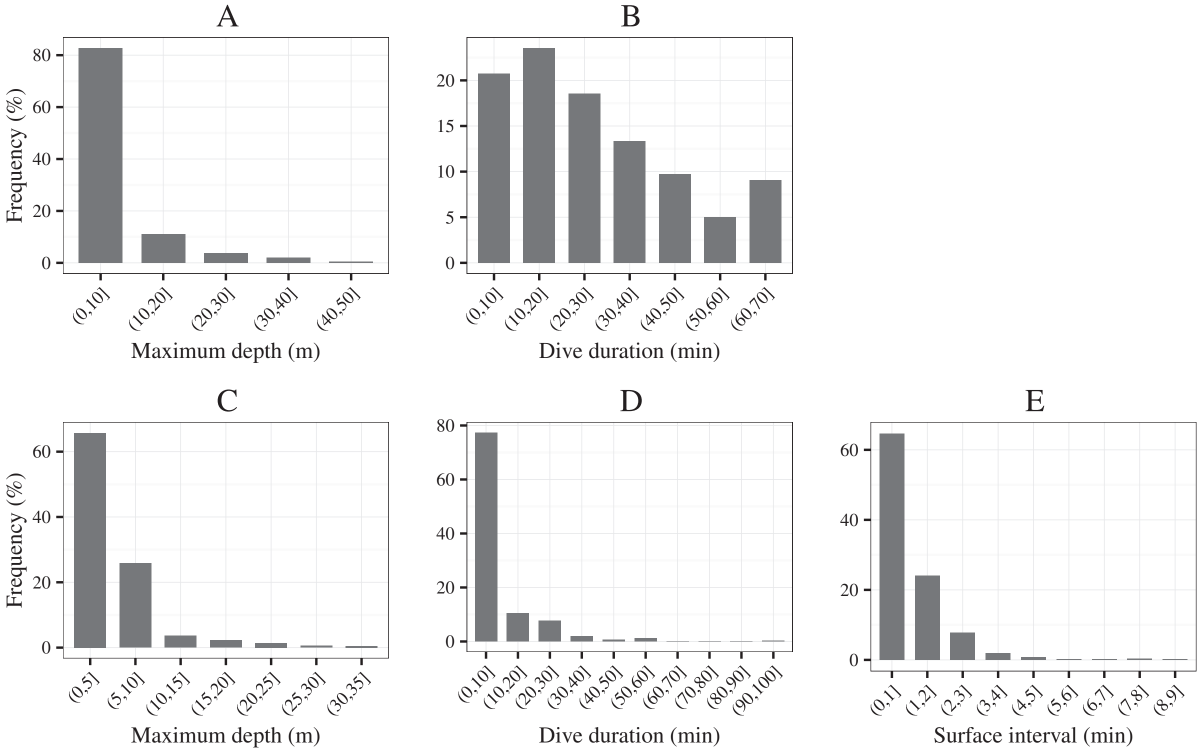

Fig. 3. Histograms of the diving variables recorded by the Argos-linked Fastloc GPS tags (A and B) and the CTD-SRDL tags (C, D and E): maximum dive depth (A and C), dive duration (B and D), and post-dive surface interval (E) for all individuals.

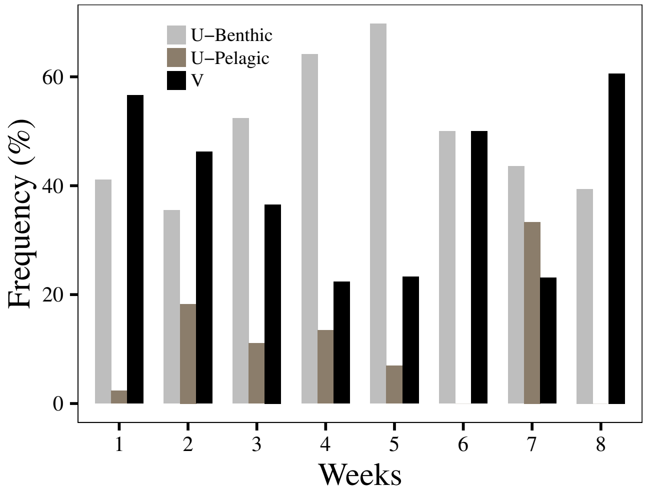

Fig. 4. Bar plots of the dive shape over weeks recorded by the six CTD-SRDL tags in 2014.

4.1. Habitat use

The kernel analysis indicated that the turtles spent most of their time in a relatively small area, covering 423 km^2 (50%). To date, the literature on the home range of this species is very limited, and only one study conducted in Central Africa has described a core range used by olive ridleys, covering 1267 km^2 (Maxwell et al., 2011), being bigger than in the present study (423 km^2). Such difference might be due to the different methods used to calculate the home range (Minimum Convex Polygon vs. kernel densities) and also to the core range definition, as in Central Africa it was defined as 80% vs. 50% in our study. Turtle movements were close to the shore, generally not crossing the 20 m isobaths and remaining in shallower waters than those previously observed in other olive ridley populations, which usually occupy waters with depths of up to 50 m (Whiting et al., 2007; Maxwell et al., 2011; Rees et al., 2012). As habitat use is dictated by metabolic rate, such behaviour could therefore reduce the costs of locomotion by limiting their movements (Slavenko et al., 2016). This assumption is reinforced by the low travel speeds found in our study (1.1 ± 0.1 km.h^{-1}), compared to those recorded by Chambault et al. (2016a,b) (2.5 ± 0.6 km.h^{-1}) during the post-nesting migration of the same individuals. The limited displacements were also highlighted by the short distances travelled, with females remaining within 19.6 ± 23.6 km from the nesting beach, which is in accordance with the findings of Maxwell et al. (2011) in Central Africa (27.7 ± 22.3 km). This behaviour is also identical to that shown by the same olive ridley population during tracking in the inter-nesting season in French Guiana in 2006–2007 (18.4 ± 2.9 km, Plot et al., 2012). This site fidelity probably enables turtles to remain in favourable conditions during oviposition, enhancing their fitness. A species which does not provide any parental care will attach great importance to its choice of nesting beach in order to favour the survival of its offspring (Kamel and Mrosovsky, 2005; Péron et al., 2013).

The prey data collected by the trawler (IFREMER, French Guiana) within the 90% kernel contour has shown the presence of crustaceans (43%), osteichthyes (39%), molluscs (8%), cnidarians (8%) and cephalopods (2%). Despite the temporal mismatch between olive ridleys tracking (From June to September) and the trawler sampling (November), the most abundant species found in olive ridleys home range were crustaceans and fish. This species is known to feed mainly on crustaceans and fish during the inter-nesting season, as demonstrated via stomach content analysis in northeast Brazil (Colman et al., 2014). Although no direct evidence of a feeding activity on such animals has been observed in French Guiana to date, the overlapping of potential resources with the distribution of olive ridleys suggests that if olive ridley were foraging during this period, their potential preys that might be available would include mostly crustaceans (43%) and fish (39%). Such behaviour would suggest that the turtles may adopt an income breeding strategy to cope with the energy loss that is inherent to reproduction and oviposition. To confirm this assumption, 3D accelerometers and cameras need to be deployed on this species, as previously carried out in green and loggerhead turtles (Fossette et al., 2012; Cheng et al., 2013), and complementary approaches such as isotopic analyses and oesophageal lavages/gut content analysis are also necessary (Hatase et al., 2006; Amorocho and Reina, 2007).

The oceanographic conditions of this habitat were warm (range: 26–33 °C) with highly fluctuating waters in terms of salinity (range: 19.5–36.4 psu). The thermal range was close to that experienced by other populations of olive ridleys nesting in Australia (23–29 °C, McMahon et al., 2007, Hamel et al., 2008) and Costa Rica (22–28 °C, Swimmer et al., 2006). However, the turtles crossed environments with varying levels of salinity that ranged from polyhaline (>18 psu) to ultrahaline (>33 psu) depending on their proximity to the shore. The turbid and low salinity waters can be explained by the large discharges coming from the Amazon River plume and other rivers that continuously flow into the French Guiana continental shelf (Jounneau and Pujos, 1988; Froidefond et al., 2002). The neritic domain off the shores of French Guiana is classified into three water classes based on their reflectance, and the olive ridleys concentrated their activity in the green waters (water column depth < 20 m isobaths) and beige waters (at the river mouths). In the latter, the levels of suspended matter are high (~115 mg.l^{-1}) and

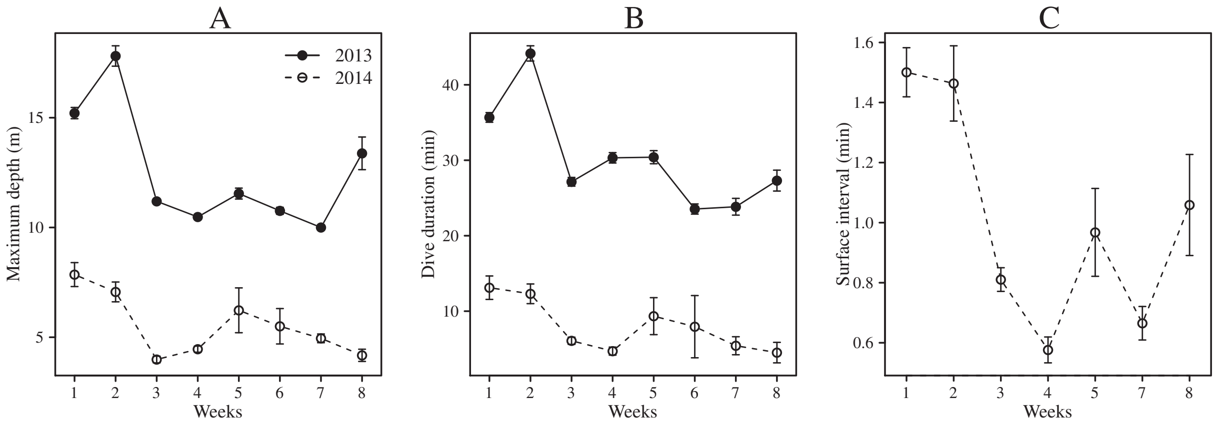

Fig. 5. Average diving variables (+SD) recorded in 2013 (filled dots) and 2014 (open dots) over the weeks of the inter-nesting season. (A) Maximum depth, (B) dive duration and (C) post-dive surface interval.

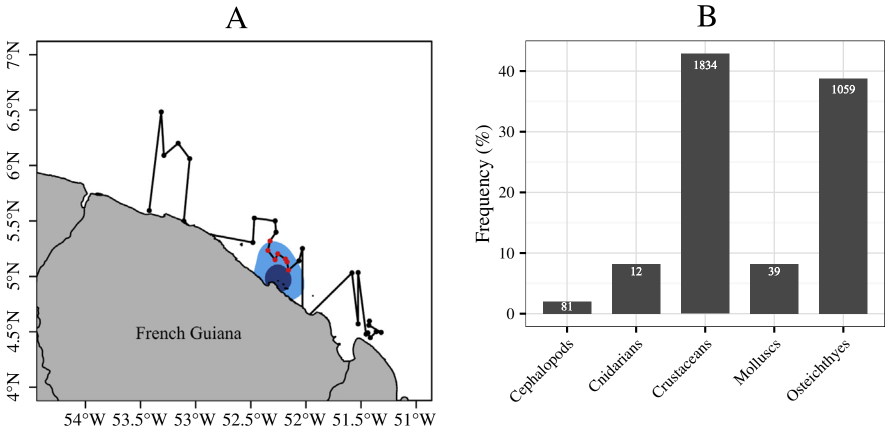

Fig. 6. (A) Trawler transect in relation to the kernel densities for 2014 (90% shown in turquoise and 50% shown in dark blue). (B) Percentage of individuals sampled for each prey group within the 90% home range in 2014 (shown by red dots in A). The white numbers in B refer to the individual abundance sampled within each group. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the chlorophyll *a* concentration is low: 2–3 mg.m^{-3} (Froidefond et al., 2002). Similar to the Kemp's ridley tracked in the Gulf of Mexico (4.5–36 psu, Metz, 2004) and the loggerhead turtles in southwest Florida (0–40 psu, Foley et al., 2006), the olive ridleys nesting in French Guiana show a high tolerance to a wide range of environments.

4.2. Behavioural shifts over the nesting season

Multiple behavioural shifts were observed in olive ridleys for both years of tag deployment, and the inter-nesting season could be divided into two phases. The distance to the nesting site increased during the first half of the period (0–21 days: 21.9 ± 24.7 km), then the turtles remained close to the beach (7.4 ± 7.8 km). The satellite tracking of the same olive ridley population followed in 2006 and 2007 indicated similar results (Plot et al., 2012), highlighting a unique reproductive synchrony in this species with individuals moving closer to the nesting beach after 21 days (Plot et al., 2012). These results reinforce the argument for a mass-nesting phenomenon, also called *arribadas*, which has been evidenced in several olive ridley populations in Mexico, Costa Rica and French Guiana (Eguchi et al., 2007; Plot et al., 2012). In French Guiana and Costa Rica, it has been reported that the inter-nesting interval of this species is approximately 28 days (Plotkin, 2007; Plot et al., 2012) and 18 days in Central Africa (Maxwell et al., 2011), which coincides with the moment when the individuals remain close to the nesting beach, i.e. 21 days after the last nesting event, and is probably related to landing synchrony (Plot et al., 2012). However, inter-annual variability has been observed, as the turtles tracked in 2014 moved closer to the nesting beach after only 14 days, indicating possible shorter inter-nesting intervals, as previously observed in other populations (Whiting et al., 2007; Hamel et al., 2008). Such variability in the inter-nesting interval could be explained by the behavioural plasticity of the females during the pre-breeding migration (i.e., a remigration interval that can last from one to two years) and by the different foraging grounds used before or during the nesting season (McMahon et al., 2007; Chambault et al., 2016a,b). Indeed, one turtle tracked in 2014 had already been observed in 2013, confirming the uncommon and short remigration interval of this species.

Some behavioural shifts were also observed in diving behaviour, and comprised the same two distinct phases that were identified in the horizontal dimension. Similar to Plot et al. (2012), the turtles performed longer (29.7 ± 21.0 min) and deeper dives (12.6 ± 7.4 m) during the first three weeks of the inter-nesting season compared to the second half of the tracking (25.9 ± 19.3 min, 10.4 ± 4.9 m). These results are consistent with other studies showing that breeding females decrease their dive duration in the few days preceding a nesting event (Hays et al., 1999; Fossette et al., 2007; Houghton et al., 2008; Hamel et al., 2008; Plot et al., 2012), and may be related to the selection of the nesting beach (Plot et al., 2012). At the beginning of the inter-nesting

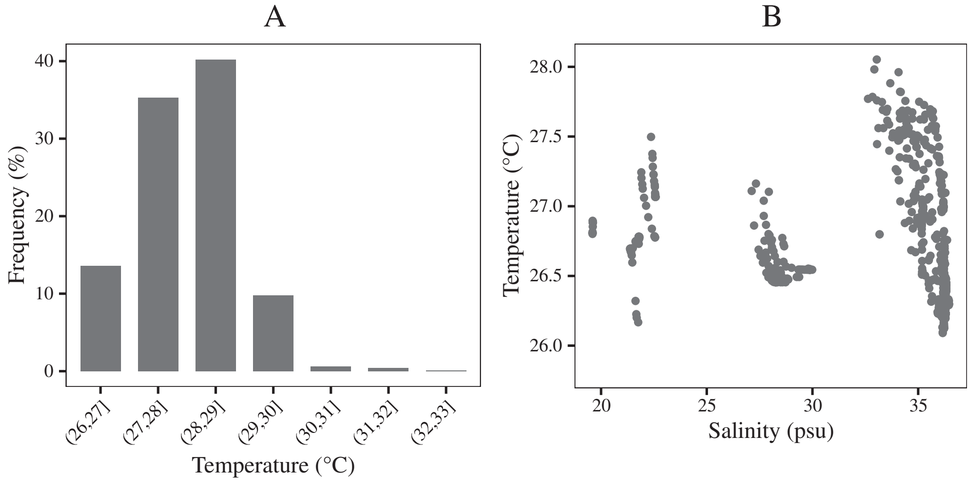

Fig. 7. (A) Histogram of the temperatures recorded by the Argos-linked Fastloc GPS tags in 2013, and (B) Temperature-Salinity diagram from the CTD-SRDL tags deployed in 2014.

season, such behaviour may indicate either a foraging or a resting activity (Hays et al., 1999; McMahon et al., 2007), especially when turtles perform mostly benthic dives (92%). This diving behaviour indicates that they follow the seabed, as previously described in leatherback turtles (Fossette et al., 2007). As olive ridleys performed mainly V-shaped dives (56%) during the first three weeks, such a pattern is more likely to be associated with exploratory behaviour and could be associated with an opportunistic feeding behaviour. In contrast, the dives were mainly benthic and U-shaped during the second half of the period (70%), which can be interpreted as either a resting or a foraging activity. Unlike the tracking during the post-nesting migration period, where the dives were mainly pelagic (Chambault et al., 2016a,b), the predominance of benthic dives in the present study excluded the use of hunting time index as a proxy for the foraging behaviour of this species within dives. Further studies therefore need to be conducted at a finer scale using 3D accelerometers on gravid olive ridleys to distinguish between these two activities during the inter-nesting season.

5. Conservation implications

The satellite tracking of these French Guianese population of olive ridleys provided crucial information on (i) habitat use and (ii) the behavioural shifts that could be used by these females during the inter-nesting season. The estuarine habitat was confined close to the shore, characterized by turbid waters that were strongly influenced by the river discharges along the Guiana coast (Froidefond et al., 2002). Such conditions make this species critically vulnerable due to reduced visibility (Metz, 2004; Chambault et al., 2016a,b) and the high energetic costs of reproduction and nesting activities during this period. The strong occurrence of illegal drifting net fisheries in the coastal area of the Guiana shield (Levrel, 2012; Cissé et al., 2014) exposes this vulnerable species to lethal interactions via bycatch (DEAL Guyane and Agence des Aires Marines Protégées, 2013). This situation requires the implementation of highly coercive but geographically localized measures in this small area (423 km^2) used by breeding turtles. A further investigation on the interactions between olive ridleys and fisheries is therefore needed to support the application of adequate measures to ensure the conservation of this threatened species.

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ANNEXE C

Tableau résumé des déplacements horizontaux des huit tortues luths suivies depuis le site de Rémire-Montjoly en Guyane française durant l'inter-ponte

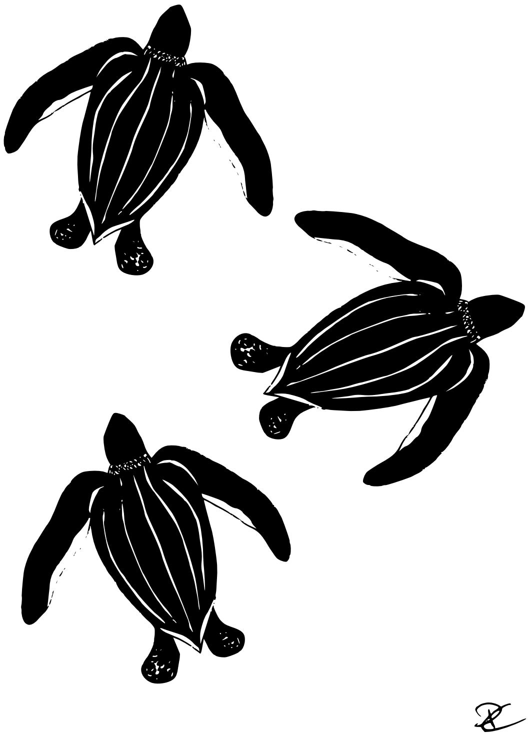

Tableau C.1 – Résumé des déplacements horizontaux des huit tortues luths suivies depuis le site de Rémire-Montjoly en Guyane française durant l'inter-ponte. PTT correspond au numéro d'identification des balises et Nloc au nombre de positions enregistrées par individu. Les valeurs correspondent aux moyennes ± SD.

PTT	**Balise**	**Date de début**	**Départ en migration**	**Nloc**	**Durée du suivi** (j)	**Distance parcourue** (km)	**Vitesse** (km.h^{-1})
131347	SPLASH10-F	27/07/2014	28/08/2014	435	32	1632	2,9±2,1
149680	SRDL	24/06/2015	29/07/2015	78	35	889	1,2±1,3
149681	SRDL	23/06/2015	05/07/2015	28	12	465	1,6±1,5
149682	SRDL	24/06/2015	17/07/2015	56	23	482	1,4±1,4
149683	SRDL	24/06/2015	16/07/2015	57	22	476	1,3±1,4
149684	SRDL	23/06/2015	05/07/2015	17	12	460	2,0±2,0
149685	SRDL	23/06/2015	14/07/2015	61	21	789	1,8±1,5
149688	SRDL	23/06/2015	07/07/2015	39	14	770	2,7±1,8
				96±138	*21±8*	*745±398*	*1,7±0,5*

ANNEXE D

Identification of key marine areas for conservation based on satellite tracking of post-nesting migrating green turtles (*Chelonia mydas*)

M. Baudouin, B. de Thoisy, **P. Chambault**, R. Berzins, M. Entraygues, L. Kelle, A. Turny, Y. Le Maho, D. Chevallier. 2015. Identification of key marine areas for conservation based on satellite tracking of post-nesting migrating green turtles (*Chelonia mydas*). Biological Conservation. 184. 36-41. 10.1016/j.biocon.2014.12.021.

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Identification of key marine areas for conservation based on satellite tracking of post-nesting migrating green turtles (*Chelonia mydas*)

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A B S T R A C T

The green turtle (*Chelonia mydas*) is classified as an endangered species on the IUCN Red List since 1986. This species is especially threatened in South America due to bycatch by fisheries along the northeastern coasts. It is particularly crucial to identify specific marine areas for conservation measures to safeguard green turtle rookeries in Suriname and French Guiana. Our study provides valuable information to attain this goal, describing the satellite tracking of post-nesting migration routes used by 16 green turtles fitted with Argos/GPS Fastloc satellite tags at the end of the nesting season. The data we obtained show a single migratory corridor: all the turtles followed a similar eastward route along the Guianan and the Brazilian coast. The GPS signal was lost for two individuals a few weeks after tracking commenced, suggesting that they were caught by fishermen. Thirteen turtles reached the coast of the state of Ceará (Brazil), where they spent at least one month. One turtle continued 700 km further to the coastal regions of Natal and Recife (Brazil), which are known feeding areas of the green turtle populations nesting on Ascension Island. The migratory corridor is essentially narrow, with a width of 22 km for most of the distance covered. It constitutes a major dynamic link between the nesting and feeding areas and crosses three Regional Management Units of the Atlantic basin. Since green turtles face a high risk of being caught in fishing nets, measures of protection should be implemented along this corridor.

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1. Introduction

Sea turtles are among the most impressive navigators of the animal kingdom. They follow migratory pathways which sometimes go across entire ocean basins (Lohmann et al., 2008). Juveniles of some species, such as loggerheads (*Caretta caretta*) and green turtles (*Chelonia mydas*), settle in neritic feeding grounds with possible seasonal migration between summer and winter habitats (Musick and Limpus, 1997; Lohmann et al., 2008). The adults of most species may migrate considerable distances from their feeding grounds to specific breeding and nesting areas (Craig et al., 2004; Ferraroli et al., 2004; Hays et al., 2002). With the exception of the breeding season, when the females lay their eggs on nesting beaches, it is however difficult to observe sea turtles in their natural environment. The tracking of individuals through the Argos Satellite system may however provide a very fine-scale analysis of the pelagic movements of this species which regularly comes up at the sea surface to breathe (Kaplan et al., 2010), allowing identification of its feeding and breeding areas and of its migration path (Schofield et al., 2010; Maxwell et al., 2011).

While the green turtle is listed as globally endangered, the state of some populations may be a cause for optimism (Seminoff and Shanker, 2008). However, similar to other marine turtles, the incidental catch of green turtles by marine fisheries leads to mortality, and the degradation of the marine and nesting habitat currently poses a great threat to this species (Seminoff et al., 2002; Wallace et al., 2013). Despite its conservation status and legal protection, poaching is also considered as a current threat (García et al., 2003; Koch et al., 2006). Overall, bycatch, habitat

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degradation, human consumption of turtle meat and eggs and the sale of their shells have led to a 48–66% decrease in green turtle populations throughout the world (Seminoff et al., 2002).

However, the current knowledge on the green turtle movement patterns is still very poor. Understanding how this species moves at sea is crucial if we hope to develop and implement more effective bycatch mitigation measures (Hays, 2008; Wallace et al., 2013).

Wallace et al. (2010) defined Regional Management Units (RMU) for all marine turtle species using multi-scale biogeography data that reflected population connectivity. The north-eastern coast of South America has been focused here because it is a major nesting site for green turtles (Seminoff et al., 2002; Wallace et al., 2010), which are relatively abundant on the beaches of Suriname and French Guiana during the nesting period (Chevalier et al., 1998). Wallace et al. (2013) assessed incidental fishing of marine turtles in RMUs and it appears that bycatch is a persistent and serious issue off the north-eastern coast of South America. For all species combined, a very high Bycatch Per Unit Effort (BPUE) was identified at the mouth of the Amazon – among the five highest percentages of global records for longline and net efforts (Wallace et al., 2013).

In the present study, we analyzed the migration of 16 turtles that were tracked by satellite during their post-nesting migration along the coasts of Suriname, French Guiana and Brazil. We determined their migration route, the distance traveled by each green turtle and their individual characteristics, and identified their migratory stopovers. Our study highlights the importance of identifying and mapping this migration corridor, which links nesting and feeding sites and crosses three RMUs (Wallace et al., 2010). Our data should provide a scientific base for decision-making processes concerning the management and conservation of protected areas for green turtles and the regional mitigation of at-sea threats.

2. Materials and methods

2.1. Tag deployment

The beaches of the east coast of Suriname and western coast of French Guiana are one of the major nesting sites for green turtles in the Atlantic basin (Schulz, 1975). In Suriname, approximately 8000 green turtle nests were counted on the Galibi beaches in 2012 (Pinas, 2013). In French Guiana, the nesting activity of the green turtle has been monitored for around 15 years, and a capture-marking-recapture program started in 2010. In 2012, around 4000 green turtle nests and almost 800 individuals were counted on the beaches of French Guiana, mainly on the Awala-Yalimapo beach (Berzins, 2014). Those two sites are now separately protected within the national nature reserves of Amana and Galibi, respectively. Yet, since some turtles use both Awala-Yalimapo (French Guiana) and Galibi (Suriname) beaches to lay during a single nesting season, those two sites might be considered as a single nesting site over the two countries.

From February 29th to June 2012, sixteen Argos/GPS Fastloc 10-F400 satellite tags (Wildlife computer. Redmond. Washington. USA. http://www.argos-system.org) were deployed on 16 adult female green turtles during the nesting season on both sides of the Maroni River: 8 turtles in Suriname (Galibi Nature Reserve beaches) and 8 turtles in French Guiana (Awala-Yalimapo, Amana Nature Reserve beaches) (53°57′W, 5°45′N). The following methods are summarized in the Fig. 1. The PTT were fixed during nesting at night, using a red light to minimize the disturbance of the turtles. First, the shell of the turtle was cleaned with scrapers, water and acetone into cleaning rags in order to remove epibiotic growth in the attachment area and obtain a clean dry working area. Secondly, the attachment area has been lightly sanded with grit sandpaper then wiped again with acetone and dried. This operation has been repeated until cloth comes up clean (Blumenthal et al., 2006; Broderick et al., 2007; Godley et al., 2002; Hawkes et al., 2007a, 2007b). The tag was then fixed with Epoxy glue as close as possible to the head, in order to secure the satellite connection at sea when the turtle breathes at the surface. As the drying time of the glue (about 2 h) was longer than the duration of nesting (about 30 min), a removable wooden enclosure was installed around the turtle to restrict its movements and delay its return to sea. The raw telemetry data were downloaded daily using the WC-DAP 3.0 software package (Wildlife Computers).

2.2. Data gathered

Data were downloaded daily via the Argos Message Retriever (WC-DAP, Wildlife Computers-Data Analysis Programs, Inc. 2010). In order to provide higher location accuracy and to increase the number of available positions, the tags were programmed to record simultaneously Argos and GPS locations (Costa et al., 2010). GPS sampling interval recorded the position of the turtle every 4 h. To each Argos location was assigned a Location Class (LC): 3, 2, 1, 0, A, B or Z. Each LC was associated to an estimated error based on the number of messages received per satellite pass: from <250 m to >1500 m (LC 3, 2, 1 and 0), no accuracy estimation (LC A and B) and invalid location (LC Z). For this analysis, LC Z were excluded as well as those on land and those separated by

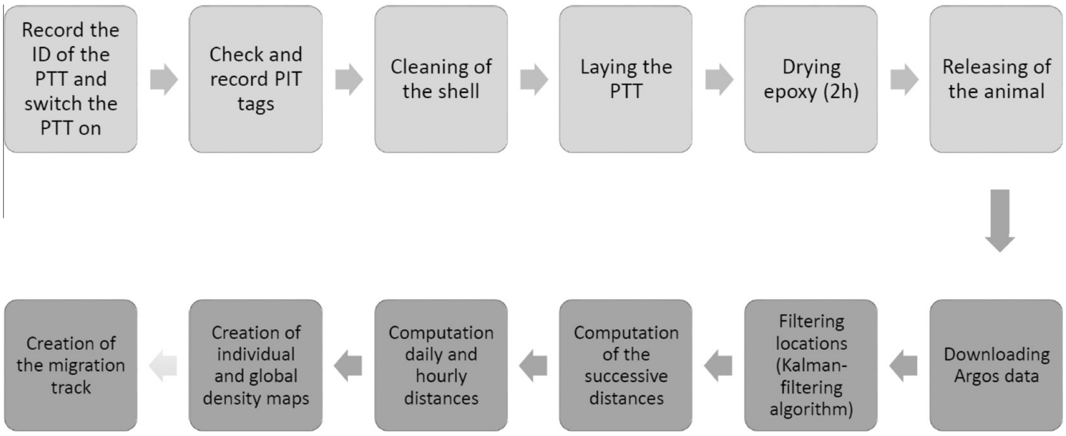

Fig. 1. Methods diagram for steps from the laying of the tag on the 16 green turtles to data analysis.

Table 1
Duration and number of positions of the 16 female green turtles equipped in the Galibi and Amana Natural Reserves in 2012.

Individual (PIT-tag)	Start	End	Duration (d)	Number of positions	Number of positions.d^{-1}
115445	May-8	August-19	103	939	11.0
115446	May-28	August-1	65	793	12.2
115447	May-23	October-24	154	1287	10.6
115448	May-8	September-1	116	1311	12.4
115449	April-26	August-18	114	979	10.5
115450	April-23	October-7	167	2129	13.5
115451	June-8	July-14	36	236	6.7
115452	April-16	August-14	120	1504	13.3
115453	April-25	June-2	38	388	15.5
115454	May-12	September-3	114	1286	12.9
115455	April-18	August-23	127	1620	15.3
115456	June-30	October-18	110	1105	12.0
115457	June-28	October-23	117	1239	12.5
115458	May-28	August-14	78	485	8.0
115459	May-28	October-24	149	1556	12.4
115460	June-13	October-7	116	1026	13.3
Average	–	–	107.8 ± 37.4	1117.7 ± 490	12.0 ± 2.3

>10 km h^{-1}. In order to record the patterns occurring during both inter-nesting and migration phases, the tags were deployed at the beginning of the nesting season and programmed to work for about 8 months.

2.3. Data pre-filtering

Only the data recorded after the last nesting were considered for the study. A Kalman-filtering algorithm was applied by CLS (CLS, Collecte Localization Satellites, Toulouse, FRANCE) to enhance the tags' positions estimates by selecting those with the minimal residual errors (Kalman, 1960; Kalman and Bucy, 1961; Rudnick and Gaspari, 2004; Van Der Merwe et al., 2004). Then a spatial query was performed via ArcGIS version 10.1 in order to identify the date of migration departure based on the distance traveled from the nesting site.

The successive distances between the locations were calculated and the data were processed to obtain the daily distances and speeds with standard deviation for all results. The distance traveled during the day was divided by the result of *final time minus initial time* of the locations.

To highlight areas of significant aggregation of green turtles across the entire migratory path, a density map was created to identify common stopover areas for all turtles, then maps of individual densities to determine stopover areas where individuals remained for longer periods (at least five days in the same area), resulting in a higher number of locations.

3. Results

3.1. General findings

The 16 green turtles were tracked between 1 and 5 months (Table 1). On average, 1118 ± 490 locations were recorded per turtle (Table 1). The migratory paths remained close to the coast (10–15 km off the coast), except when crossing the Amazon river plume, which pushed individuals 30–200 km away from the coast (Fig. 2). The corridor formed by the sum of the individual paths had a width of approximately 22 km on average, with differences at the mouth of the Amazon where some turtles stayed near the coast and others moved up to 200 km offshore (Fig. 2). Positions were recorded for individual no. 115450 over a very long period, with 167 days of tracking. The tracking was however interrupted after a only couple of weeks for two individuals.

3.2. Distances traveled

3.2.1. Total distance

On average, the 16 turtles traveled 3683 ± 1007 km. Turtle no. 115453 traveled the shortest distance (1360 km), whereas individual no. 115450 traveled 5278 km (Table 2).

3.2.2. Daily distances

The average daily distance of all tracked turtles was 42.7 ± 8.7 km (Table 2). For each turtle, the average daily distance varied from 33.4 km to 61.1 km (Table 2, no. 115450 vs. 115460 respectively) and was significantly different between individuals (ANOVA, $F_{15,75165} = 3.314$, $p < 0.001$).

3.2.3. Hourly speed & distance

On average, the green turtles moved at 1.6 ± 0.2 km h^{-1} (Table 2). Tracked individuals traveled at an average speed of 1.3 ± 1.7 km h^{-1} to 2.1 ± 2.2 km h^{-1} (Table 2, no. 115449 vs. 115451 respectively), and speed was significantly different between turtles (ANOVA, $F_{15,437} = 7.526$, $p < 0.001$). However, much higher speeds were also identified, with bursts of speed attaining 10 km h^{-1}.

3.3. Migratory stopovers

The number of stopovers obtained for each turtle varied from zero to five. Among the 16 turtles, only four did not make any stopover at all during their migration. On average, the other green turtles made 3.5 ± 1.8 stopovers during their journey.

Six main stopover areas were highlighted (Fig. 2): one along the Guianese coast, the second at the estuary of the Oyapock river (border between French Guiana and Brazil), the third before the mouth of the Amazon, a fourth just after the mouth of the Amazon, the fifth on the coast of the state of Maranhão, and the sixth on the coast between the states of Piauí and Ceará (Brazil). The first three were the most frequented, with five to seven turtles stopping there.

3.4. Final area

The end of the long migration of the turtles was marked by their arrival along the coast of the state of Ceará (Brazil). Whatever their individual date of arrival, all the individuals stayed in this area between June and October. On reception of the last Argos signal, most turtles had already been there for over a month.

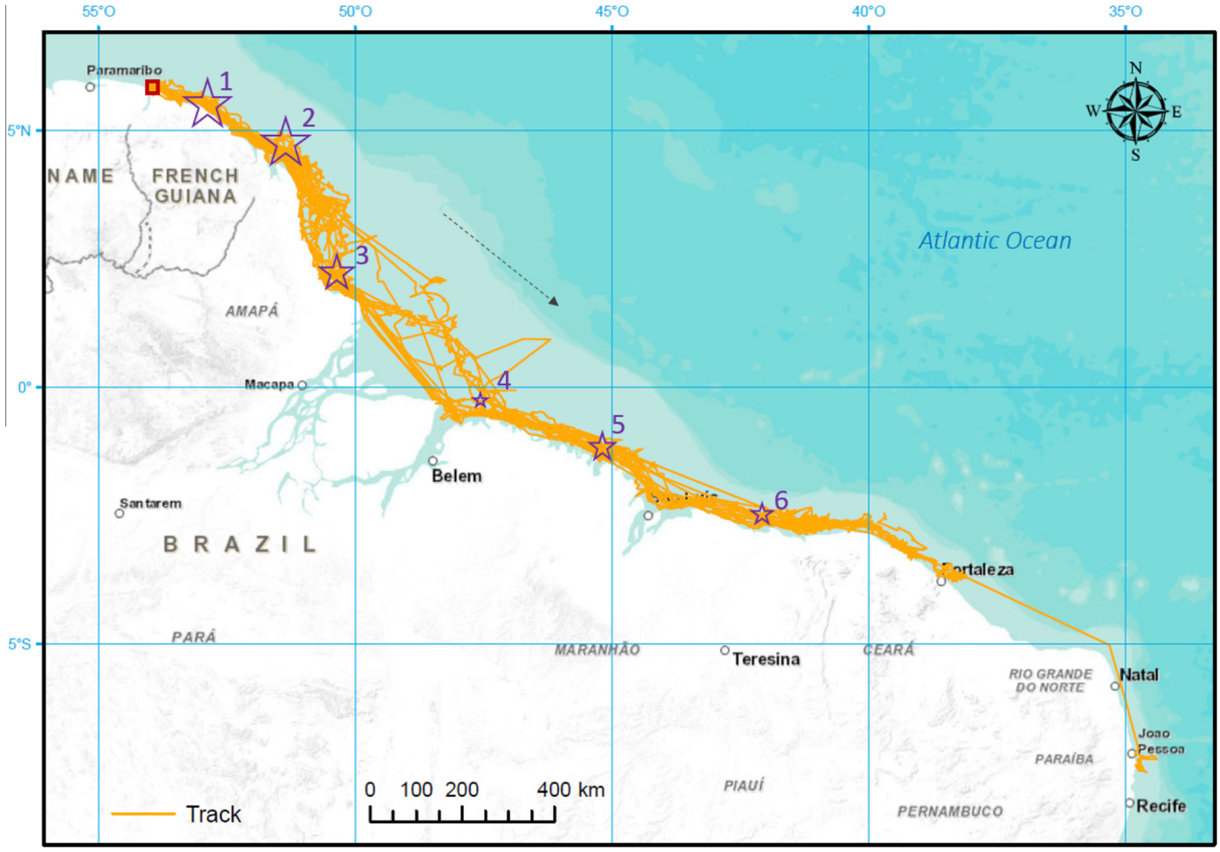

Fig. 2. Tracking of 16 green sea turtles along the north-eastern coast of South America. The red square indicates the starting location and the arrow shows the direction of their migration from the nesting sites in French Guiana and Suriname. The areas of particular interest (stopovers) are indicated by stars that are proportional to the number of turtles remaining in these areas, at least 5 days during their travel (in order: 7, 7, 5, 2, 4, and 3). (For interpretation of the references to color in this Fig. 2 legend, the reader is referred to the web version of this article.).

Table 2

Total distance, daily distance and speed of the 16 female green turtles equipped in the Galibi and Amana Natural Reserves in 2012. The total distances are in km, daily distances in km d^{-1} and speeds in km h^{-1}.

Ptt	Total distance	Daily distance	Speed	Maximum speed
115445	3578	42.1	1.6 ± 2.0	9.8
115446	3090	47.5	1.8 ± 2.0	10.0
115447	4268	35.3	1.3 ± 1.8	9.9
115448	4175	39.4	1.6 ± 2.0	9.9
115449	3306	35.6	1.3 ± 1.7	9.8
115450	5278	33.4	1.4 ± 1.9	10.0
115451	2071	59.2	2.1 ± 2.2	9.5
115452	4488	39.7	1.7 ± 2.0	9.8
115453	1360	54.4	1.8 ± 2.1	9.6
115454	3826	38.3	1.5 ± 2.0	9.8
115455	4019	37.9	1.5 ± 1.9	9.8
115456	3287	35.7	1.3 ± 1.9	10.0
115457	3849	38.9	1.5 ± 2.0	9.7
115458	2939	48.2	1.6 ± 1.9	9.9
115459	4692	37.5	1.6 ± 2.1	10.0
115460	4706	61.1	1.6 ± 2.0	9.8
Average	3683 ± 1007	42.7 ± 8.7	1.6 ± 0.2	9.8 ± 0.1

4. Discussion

This is the first detailed study of the post-nesting migration of green turtles on the Guiana Shield, and it includes paths, travel distances, speed and stopovers. These data may therefore contribute to improve our general understanding of sea turtles migratory patterns and to better define the regional conservation strategy of this endangered species.

The migration path closely follows the northeastern coast of South America (generally less than 15 km from the shore, except in the vicinity of the Amazon). This supports the idea that the populations of green turtles nesting on the continent remain on the continental shelf during their post-nesting migration (Godley et al., 2007). While all sixteen turtles followed the same path, high inter-individual variations were observed in the total distances traveled, and also a great heterogeneity in the daily distances of a single animal journey. This suggests different movement behaviors during migration that could be related to the different environmental conditions (currents, food resources, predation, *etc.*) met by each turtle at some time during their journey. The hourly distances traveled by green turtles are in accordance with the existing literature (Table 3; Cheng, 2000; Cheng et al., 2009; Craig et al., 2004; Godley et al., 2002; Hays et al., 1999; Luschi et al., 1998; Luschi et al., 1996; Seminoff et al., 2008; Troëng et al., 2005). We observed that during crossing the plume of the Amazon, some turtles followed trajectories away from coast. At this location, eddies are created from the North Brazil Current, moving at a velocity that can exceed 1 m s^{-1} (Ffield, 2005). Furthermore, the plume of the Amazon has a surface current which can also exceed 1 m s^{-1}, depending on the winds (Nikiema et al., 2007). Although these global currents generally have a northwestern direction and therefore flow directing towards the migrating green turtles, their direction can change locally depending on the tides and the strength of tradewinds (Nikiema et al., 2007). Seminoff et al. (2008) and Cheng et al. (2009) showed the influence of surface currents on the movements of green turtles and revealed that they could swim either in concordance with or against some currents or eddies.

Table 3
Track duration (d), total distances (km) and speeds (km h^{-1}) of post-nesting migrations for green turtles throughout the world.

Season	Ocean (Country)	Number of turtles	Duration	Total distance	Speed	Citations
1993 to 1995	West Pacific (American Samoa)	7	40	1599	1.80	Craig et al. (2004)
1998–1999	Mediterranean (Cyprus)	6	8–44	1364	1.98	Godley et al. (2002)
1994	West Pacific (Malaysia)	4	25.5	1135	–	Luschi et al. (1996)
1997	Central Atlantic (Ascension)	6	35	1968	2.59	Luschi et al. (1998) and Hays et al. (1999)
2003 and 2005	East Pacific (Ecuador - Galàpagos)	12	65.6	1657	–	Seminoff et al. (2008)
1994 to 1997	West Pacific (Taïwan)	8	188.8	193–1909	1.2–2.8	Cheng (2000)
1996 to 2004	West Pacific (China)	6	20	1204	0.80	Cheng et al. (2009)
2000 to 2002	West Atlantic (Costa Rica)	10	265.3	753.6	2.2	Troëng et al. (2005)

We identified six areas of migratory stopovers for the sixteen turtles. The green turtle is a capital breeder: it builds up energy reserves before migration in specific feeding areas, and does not feed during the nesting period (Hays et al., 1999). These stopovers areas (and particularly the first three, which are widely used) are probably used by turtles for occasional resting and feeding in order to build the body fuels requested to undertake their migration and lead them to a preferential feeding area. This kind of strategy has been observed for this species during coastal migration in the Mediterranean Sea (Godley et al., 2002) and in the Pacific Ocean in Asia (Cheng, 2000): in both cases, turtles fed several times during their migration. The adult green turtle is strictly herbivorous, and spends most of its life in coastal feeding areas (Senko et al., 2010) consisting of sea grass beds in shallow waters (Hirth, 1997; Bjorndal, 1985). A detailed study of turtle behavior at stopover sites would be useful to clarify the importance of these hotspots in the conservation of green turtles. It would also be of interest to determine if the green turtles make the same stopovers each year; i.e. at the same localizations we pinpointed in this study.

The fact that post-nesting green turtles from French Guiana and Suriname may spend more than one month at their final destination is also of great importance for their conservation. This suggests either the possibility of a long stop after this journey to restore body fuels and reach the body condition requested to keep traveling further south, or until the arrival at their migratory destination. That one individual (no. 115460) continued its migration to a site on the coastal regions of Natal and Recife (Brazil), which is also an area used for feeding by the green turtle population nesting on Ascension Island (Hays et al., 2002; Luschi et al., 1998), making it a key area in the spatial ecology of green turtles from the southern Atlantic. Hays et al. (2002) showed that the green turtles from Ascension Island move spontaneously towards the Brazilian coast before continuing their migration along these Brazilian coasts, ignoring the areas with abundant food resources that are available in the early stages of their journey. Food availability might therefore not be the only selection criterion and in addition to the quality and quantity of food available. In this case, other abiotic factors could influence the decision of sea turtles to stop and stay in these areas, or move further away.

The migration patterns observed in the present study should also be analyzed in relation to the location and intensity of fisheries and therefore the risk of bycatch for the migrating turtles. For two of our sixteen turtles, the tracking was interrupted before the depletion of the GPS satellite tag batteries. Yet, the tag has operated during a few weeks for one of them, indicating that it was brought ashore in a Brazilian fishers village and therefore that it had been accidentally caught by fisheries. Interestingly, this interruption occurred around the mouth of the Amazon, where bycatch is known to occur with longlines and gillnets (Wallace et al., 2013). However, Wallace et al. (2013) do not include the effect of coastal gillnet fishing, which is widespread on the Brazilian coast and difficult to assess (see Bioinsight and DIREN Guyane, 2003; Chevalier et al., 1998).

This corridor from eastern Suriname border to northeastern coast of Brazil is crucial because it could connect the Atlantic South Caribbean, Atlantic Southwest and Atlantic South Central RMUs (Wallace et al., 2010). Thus, one can see here that, rather than dealing with each RMU individually, it would be wiser to evaluate the potential connections between these units, and build a consistent and applicable global management strategy for all three RMUs.

5. Conclusion

This study provides detailed information about the post-nesting migratory paths of green turtles nesting at the border between French Guiana and Suriname, describes the areas used by turtles (resting areas) along the Brazilian coast and identifies the hot spot that appears to be their goal at the end of their travel. A high rate of bycatch occurs along this migratory path (Davies et al., 2009; Wallace et al., 2013) and could have a substantial impact on the green turtle population. The next step should be to investigate how far legal and illegal fishing overlap with the paths and final destination of migrating turtles. Finally, as at least two turtle populations use the same feeding area, the efficient protection of foraging areas of turtles along the extensive Brazilian coast may then consolidate populations thousands of kilometers away (Naro-Maciel et al., 2007). International conventions, regional protection plans and transnational actions such as those already implemented in Argentina (González-Carman et al., 2012) or in the state of Sergipe in Brazil (Coelho Dias da Silva et al., 2010) should be also applied in these foraging areas of green turtles if we want to ensure the conservation of this species.

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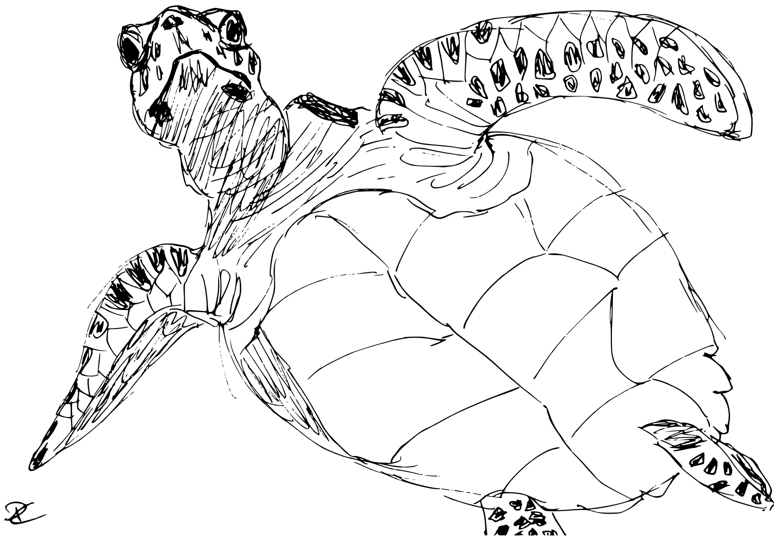
ANNEXE E

Dispersal and diving adjustments of the green turtle *Chelonia mydas* in response to dynamic environmental conditions during post-nesting migration

P. Chambault, D. Pinaud, V. Vantrepotte, L. Kelle, M. Entraygues, C. Guinet, R. Berzins, K. Bilo, B. de Thoisy, Y. Le Maho, D. Chevallier. 2015. Dispersal and diving adjustments of the green turtle Chelonia mydas in response to dynamic environmental conditions during post-nesting migration. PLoS ONE. 10(9). 10.1371/journal.pone.0137340.



RESEARCH ARTICLE

Dispersal and Diving Adjustments of the Green Turtle *Chelonia mydas* in Response to Dynamic Environmental Conditions during Post-Nesting Migration

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Abstract

In response to seasonality and spatial segregation of resources, sea turtles undertake long journeys between their nesting sites and foraging grounds. While satellite tracking has made it possible to outline their migration routes, we still have little knowledge of how they select their foraging grounds and adapt their migration to dynamic environmental conditions. Here, we analyzed the trajectories and diving behavior of 19 adult green turtles (*Chelonia mydas*) during their post-nesting migration from French Guiana and Suriname to their foraging grounds off the coast of Brazil. First Passage Time analysis was used to identify foraging areas located off Ceará state of Brazil, where the associated habitat corresponds to favorable conditions for seagrass growth, i.e. clear and shallow waters. The dispersal and diving patterns of the turtles revealed several behavioral adaptations to the strong hydrodynamic processes induced by both the North Brazil current and the Amazon River plume. All green turtles migrated south-eastward after the nesting season, confirming that they coped with the strong counter North Brazil current by using a tight corridor close to the shore. The time spent within the Amazon plume also altered the location of their feeding habitats as the longer individuals stayed within the plume, the sooner they initiated foraging. The green turtles performed deeper and shorter dives while crossing the mouth of the Amazon, a strategy which would help turtles avoid the most turbulent upper surface layers of the plume. These adjustments reveal the remarkable plasticity of this green turtle population when reducing energy costs induced by migration.

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Data Availability Statement: As the studied species Chelonia mydas is classified as endangered on the IUCN Red List, location data are available upon request by contacting DC at damien.chevallier@iphc.cnrs.fr. The diving data are available on Dryad, doi: http://datadryad.org/review?doi = doi:10.5061/dryad.b35g2.

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Introduction

Seasonality drives the availability and aggregation of resources, and is thus one of the main ecological factors affecting the evolution and the ecology of long-distance migrants [1]. Indeed, in most cases, the requirements of migratory animals temporally and spatially match the peak of resource abundance, thus avoiding resource depletion. Migrant organisms time their movements according to their life stages and their different activities (growth, breeding, etc.) in order to exploit seasonal resources that vary at temporal and spatial scales, generally travelling long distances to reach appropriate sites for their needs [2]. It is crucial to assess the dispersal movements and the habitat used by migrating animals in order to understand their ecology and facilitate the implementation of adequate conservation policies [3]. This migratory behavior has been studied in a wide range of marine groups such as mammals [4,5], birds [6], fish [7,8] and reptiles [9–11].

Sea turtles are long-distance migrants that undertake long journeys from their nesting sites to foraging grounds [12]. Most nesting sites do not provide sufficient energy resources for turtles to sustain oviposition and year-round residency [10]. Additionally, the turtle allocates the majority of its energy to reproduction during breeding and nesting, resulting in high energy requirements at the end of the nesting season [13,14]. The turtles therefore migrate after the nesting season to replenish their body reserves, foraging in areas of high productivity in order to maximize their foraging efficiency.

The migratory strategy associated with specific foraging grounds varies greatly across sea turtle populations [15]. Most of adult Cheloniidae, i.e. hawksbill, loggerhead, and green turtles, usually migrate across the open ocean to reach neritic feeding grounds [16]. However, while satellite tracking has made it possible to outline the migration routes, we still have little knowledge of how sea turtles select their foraging grounds [17].

Adult Cheloniidae sea turtles feed on different resources, depending among others on their ecological requirements, their diet and on the habitat characteristics, i.e. resource availability, competition, etc. Unlike the omnivorous (olive ridley and hawksbill) and carnivorous (loggerhead) species of sea turtles [18], the green turtle *Chelonia mydas* is mainly a herbivorous grazer at the adult stage, and is therefore dependent on seagrasses or algae meadows [18]. A high diversity of seagrass species [19] can be found throughout the western part of the Tropical Atlantic from the Gulf of Mexico to the north part of the Brazilian coast (up to 10°S). These marine meadows provide foraging grounds for several green turtle populations [20] originating from seven different rookeries: Ascension Island, Matapica (Suriname), Aves Island (Venezuela), X'cacel and Isla Cozumel (Mexico), Tortuguero (Costa Rica) and the east coast of Florida in the United States [20].

In addition to these seven populations, there is another little-known rookery in the western Equatorial Atlantic, located at the natural border between French Guiana and Suriname along the beaches of the Maroni estuary [21]. Since seagrass is distributed throughout the Tropical Atlantic [19], there is a possibility that turtles from this nesting site could either migrate northwestward, following the Guiana current flow to reach high density seagrass beds found in the Caribbean, or swim along the Brazilian coasts further south [19,22]. Baudouin et al. (2015) found that they undertake a south-eastward migration, presumably swimming against the strong North Brazil current and crossing an unfavorable and highly turbulent zone, the Amazon River plume.

The Amazon River is a major source of freshwater input, supplying 20% of the freshwater entering the ocean [23]. It has the highest level of water and sediment discharge and the largest drainage basin in the world [23–25]. The Amazon plume discharges 115.10^7 tons of sediments into the Equatorial Atlantic Ocean per year, strongly influencing the oceanographic and biochemical processes of the north-eastern American coast [24–26]. The large amounts of suspended materials carried by the plume lead to low levels of irradiance, hampering phytoplankton photosynthesis [27]. *A priori*, such turbid waters are therefore an unsuitable foraging habitat for herbivorous organisms [28].

If green turtles cross this particularly turbulent zone as part of their migratory strategy, there must be a reason for undertaking this long and counter-current migration to reach specific areas off the Brazilian coast. Our study is based on satellite telemetry, and attempts to shed light on how green turtles nesting in French Guiana and Suriname select their foraging grounds and adapt their post-nesting migration to dynamic environmental conditions. Our two main objectives in this study of green turtle migration strategy were therefore (i) to locate the foraging grounds and characterize habitat affinities and (ii) to assess how oceanographic conditions encountered along the way can affect the movements of turtles in terms of dispersal and diving patterns.

Materials and Methods

Ethics statements

This study meets the legal requirements of the countries where this work was carried out, and follows all institutional guidelines. The protocol was approved by the "Conseil National de la Protection de la Nature" (CNPN, http://www.conservation-nature.fr/acteurs2.php?id=11), a branch of the French ministry for ecology, sustainable development and energy (permit Number: 09/618) acting as an ethics committee in French Guiana and Suriname. After the evaluation of the project by the CNPN, fieldwork was carried out in strict accordance with the recommendations of the Police Prefecture of French Guiana, Cayenne, France, in order to minimize the disturbance of animals.

Satellite tag deployment

During the inter-nesting season, 16 Argos-linked Fastloc GPS tags (MK10, Wildlife Computers Redmond, WA, USA) were deployed on adult female green turtles from February to June 2012 on both sides of the Maroni River: at Awala-Yalimapo in the Amana Nature Reserve, French Guiana (5.7°N-53.9°W, $n = 8$), and in the Galibi Nature Reserve in Suriname (5.4°N-53.5°W, $n = 8$) [21]. During the same period in 2014, 10 additional females in the Amana Nature Reserve were equipped with Conductivity Temperature Depth-Fluorometer Satellite Relayed Data Loggers (CTD-SRDL, Sea Mammal Research Unit, University of St. Andrews, Scotland). The attachment procedure followed the standard methods described in Baudouin et al. [21]. During tag deployment, measurements of the Curved Carapace Length (CCL) were taken, and body mass could then be calculated using Hays et al.'s method [29]–see S1 Table.

Data collected

The procedure to extract migratory route data was identical to that used in Baudouin et al. [21]. The Argos-linked Fastloc GPS tags also provided diving data, i.e. maximum dive depths, dive durations and *in situ* temperature data, binned as 4-hour period histograms. Maximum depths were collected in different bins, every 10 m from 10 to 100 m, then every 50 m from 100 to 250 m. Maximum dive durations were stored from 30 s to 1 min, then every minute from 1 to 5 min, and finally every 10 minutes from 10 to 60 min. *In situ* temperatures were recorded during dives from 20 to 32°C, every one degree Celsius. Tags also supplied Time At Depth (TAD) and Time At Temperature (TAT), defined as the proportion of time (in %) spent at each depth and the temperature range, respectively.

The CTD-SRDL tags provided the locations of animals, i.e. Argos data, and simplified profiles of the diving parameters, and oceanographic data. However, the oceanographic and diving data were not used in the analysis.

Data pre-filtering

In order to retain only the positions recorded during the migration, a spatial query was performed via ArcGIS version 10.1 to identify the date migration began. By calculating the average daily speed during the inter-nesting season, a speed filter of 30 km.d^{-1} was set, and only the positions associated with a daily speed > 30 km.d^{-1} were set to migration phase and then retained for the analysis.

Using the same approach as described in Heerah et al. [30], a Kalman-filtering algorithm was then applied (*CLS*, *Collecte Localisation Satellites*, Toulouse, France) to enhance tag position estimates (Argos and GPS) by accounting for Argos location errors [31,32]. The shoreline was extracted from NOAA National Geophysical Data Center, Coastline, e.g. WVS, GSHHG. The General Bathymetric Chart of the Oceans database (GEBCO, http://www.gebco.net/, 30-arc-second 1 km grid) was used to discard any locations on land. The positions associated with a speed of over 10 km.h^{-1} and those with location class Z (0.1%, class associated with the raw location before Kalman filtering) were also removed, considered insufficiently accurate, and any dive depth records from tags over 100 m were also removed due to the substantial differences between the depth values provided by the pressure sensors of the tags and bathymetry data. Seven individuals (#115451, #115453, #130766, #130769, #130776, #131354 and #131355) were discarded from the analysis due to insufficient data caused by transmission issues.

First Passage Time analysis

After proceeding with pre-filtering, First Passage Time (FPT) analysis was performed on location data (Argos location after kalman filtering and GPS) in order to spatially and temporally identify Areas of Restricted Search (ARS) using R software version 3.2.1 [33]. FPT is defined as the time required by an organism to cross a circle of a given radius. FPT approach is a three-step procedure:

1. The track of each turtle was linearly interpolated at 1 km intervals whilst retaining raw locations to avoid losing data.
2. FPTs were then calculated at every location of the interpolated tracks for radii ranging from 1 to 400 km to ensure the coverage of large foraging movements [34]. For each track, the relative variance of FPT (after log transformation) was plotted against radii to identify the scales of searching activity (ARS) revealed by a peak of variance at a specific radius (S1a Fig). If several peaks appeared, we only considered the peak corresponding to maximum variance, as the study focuses on the smallest foraging scale.
3. Finally, by plotting the FPT at the optimal scale as a function of time, the periods featuring ARS (higher FPT) could be identified throughout the trip [35–37]–see S1b Fig. Temporal detection of ARS periods was carried out using Lavielle's segmentation method [38] from the *adehabitatLT* package, which allowed to differentiate between twomodes: No ARS (low FPT, transiting mode) vs. ARS (high FPT, foraging mode). The migratory mode of turtles (No ARS vs. ARS) was then inferred to each position after identifying temporal ARS locations from FPT outputs (S1b Fig).

Track segmentation

When considering the transiting mode only, the trajectories were delineated into three phases to take into account the influence of the Amazon River plume on the horizontal and vertical movements of turtles (Phase 1: before plume, Phase 2: within plume and Phase 3: after plume).

Along the tracks of the turtles, the trajectories were segmented based on the distribution of the diffuse attenuation coefficient at 490 nm (hereafter called K_d in m^{-1} –see S2 Fig). The K_d 490 nm is a standard ocean color product of downwelling irradiance at 490 nm, operationally provided by the various ocean color sensors, and considered as a good index for qualifying the light attenuation of the visible light in the water column. Averaged monthly data for K_d, an indicator of the turbidity of the water column, were extracted at a 4 km resolution from the Ocean Color website (http://oceancolor.gsfc.nasa.gov/).

Spatial analysis

For the spatial analysis, the distance travelled and the elapsed time between locations were calculated using the *trackDistance* function from the *trip* package on R [39]. The observed speed was then derived from the distance and time elapsed between locations. The distance to shore was also calculated within each of the three phases for the 19 individuals retained for the study. To investigate the role of oceanic circulation on turtle movements, surface current data (meridional and zonal components) were extracted daily for the tracking period from Mercator-Ocean GLORYS-2v1 (Global Ocean ReanalYsis and Simulations, available on: http://marine.copernicus.eu/web/69-myocean-interactive-catalogue.php) model, at a 0.25° resolution (~28 km). Oceanic current velocity and the associated direction were then derived from meridional and zonal components (scalars u and v respectively). The average swimming speed of the turtles was then calculated with correction for current velocity following Gaspar et al.'s method [40], giving a proxy of the swimming effort.

The time taken by each turtle to reach the foraging grounds (hereafter called FG) was derived from FPT outputs (S1 Fig). To assess the effects of the plume on the overall migration, we performed linear models using the time spent within the plume (TimePhase2) as a response variable, using the *lm* function from the *stat* package on R. Since the significantly lower number of locations recorded within the plume did not permit the precise calculation of the observed speed, we decided to use duration within the plume instead of the travel speed. We therefore selected one *temporal variable*, i.e. the time taken to reach a foraging ground, one *spatial variable*, i.e. the minimum longitude of the foraging ground (location of the closest foraging site reached in relation to the nesting site), one *variable relative to the movement of turtles*, i.e. the averaged swimming speed of turtles within the plume, and one *intrinsic covariate*, i.e. the body mass. Indeed, given the strong hydrodynamic forcing generated by the Amazon River plume, it can be assumed that the time taken to reach the foraging ground will increase with increasing time within the plume. In addition, we assumed that the first turtles that stop to forage, i.e. at the closest recorded foraging ground in relation to the nesting site, would have spent more time crossing the plume. Finally, we assumed that the time within the plume would increase with higher current velocity, and, conversely, would decrease with increased swimming speed. Following the method described in Zuur et al. [41], all combinations of collinear predictors (Spearman coefficients > 0.8 and < -0.8) were excluded, then all possible combinations without interactions were tested and the model with the lowest Akaike Information Criteria (AIC) was selected.

Habitat affinities

To characterize the foraging habitat in relation to environmental conditions, four static and dynamic remotely sensed variables were selected according to their biological relevance and availability in the study area. We extracted bathymetry data from GEBCO, then used the *terrain* function from the *raster* package [42] to derive the slope and obtain an indicator of seabed roughness. Two oceanographic variables were also extracted from Ocean Color website, namely K_d and Sea Surface Temperature (SST, 11 micron per day, http://oceancolor.gsfc.nasa.gov/cms/). The monthly data provided were already averaged at a 4 km resolution. A full coverage of the satellite remote sensing data over the whole area of interest could not be obtained, mostly due to cloud coverage or failures of the atmospheric correction procedure. Missing satellite data were therefore estimated by interpolating the SST and K_d using inverse distance weighting method from *gstat* and *raster* packages [42,43]. The covariate values were then extracted at the locations of each turtle (the GPS and Kalman filtered Argos locations) using the *extract* function from the raster package [42].

Diving behavior analysis

For the Argos-linked Fastloc GPS tags, no precise location was associated with each dive as diving data were stored in 4h-histograms. FPT could not therefore be applied to these data. To differentiate the diving data between the two behavioral modes, i.e. transiting vs. foraging, we therefore relied on the starting date of the foraging behavior, as identified by FPT analysis. The position data obtained from the diving records were then segmented into two modes, i.e. transiting vs. foraging. To assess the effect of the plume on diving behavior during the transiting mode, the positions were also segmented into three phases based on the K_d distribution, i.e. before plume, within plume and after plume. As the CTD-SRDL tags provided a very small amount of diving data, only data provided by the Argos-linked Fastloc GPS tags were included in the diving behavior analysis.

Statistical analyses

All statistical analyses were performed using R software version 3.2.1 [33]. All samples submitted to statistical tests were first checked for normality and homogeneity of variances by means using Shapiro-Wilk test. Depending on the results, parametric or nonparametric tests were used. Globally, Wilcoxon-Mann-Whitney tests were used to compare the diving behavior and the environmental variables between the two modes, i.e. transiting vs. foraging, using a significance level of $\alpha = 0.05$. Tukey HSD tests were used to compare the behavior between the three migration phases. Values are means ± SD.

Results

Foraging grounds selection

Foraging ground locations and spatial scales. For both years of tag deployment, the 19 analyzed tracks of *Chelonia mydas* showed a south-eastward migration over an average 3450 ±701 km for a mean tracking duration of 118±37 days (Fig 1 and S1 Table). All turtles used a narrow corridor (mean: 22.5±24.4 km), remained on the continental shelf (< 100 m isobaths) and migrated at an average observed speed of 0.5 ± 0.5 m.s^{-1} (~2 km.h^{-1})–see Table 1.

FPT analysis was used to locate the foraging areas both in time and space (S1 Fig). With the exception of one turtle that stopped off the coast of Cayenne in 2012 (#115446, foraging event in Phase 1) rather than at the very end of turtle tracks, the searching activity recorded spans from June to mid-September, and foraging areas were found to be located at the very end of the turtle tracks, along the shores of Ceará and Paraíba states, Brazil (Fig 1 and S1 Table). The radii of the foraging areas ranged from 7 to 60 km (#115448 vs. #115446), with an average of 19.7 ±14.6 km over the whole foraging trip. Twenty-one percent of the turtles used fine-scale foraging (<10 km radius, #115448, #115456, #115458 and #115460), 47% foraged on a medium-scale (10–20 km, #115445, #115449, #115450, #115452, #115454, #115455, #115457, #130767 and #130773), and 21% showed coarser-scale foraging beyond a radius of 20 km (#115446,

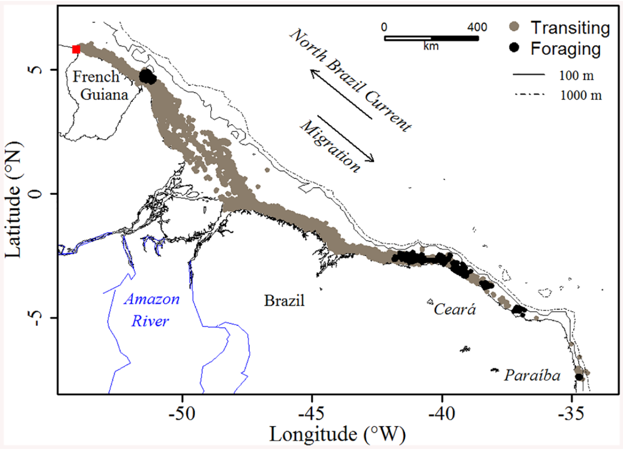

Fig 1. Locations of the 19 green turtles equipped in 2012 and 2014 for the two behavioral modes, i.e. transiting (gray) and foraging (black). The red square indicates the migration departure point. The shoreline was extracted from NOAA National Geophysical Data Center, Coastline.

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#115447, #115459 and #130770), while First Passage Time analysis revealed a complete absence of foraging behavior in two individuals (#130768 and #130771) (S1 Table).

Habitat affinities. During their migration, green turtles crossed highly contrasted environmental conditions (Fig 2). In the foraging mode, the SST was significantly lower than in the transiting mode (27.0±0.4 vs. 28.3±0.6°C, respectively, Wilcoxon test $p < 0.001$)–see Figs 2A and 3A. Identically, the K_d was significantly lower at the foraging grounds (0.09±0.09 vs. 0.41 ±0.38 m^{-1}, respectively, Wilcoxon test $p < 0.001$, Figs 2B and 3B). In contrast, the bathymetry was slightly deeper outside the feeding grounds (15.2±31.9 vs. 14.2±9.2 m, respectively, Wilcoxon test $p < 0.001$, Fig 3C). The slope remained weak over the whole migration but was slightly steeper at the foraging grounds (0.13±0.28 vs. 0.12±0.10 m, respectively, Wilcoxon test $p < 0.05$, Fig 3D).

Diving behavior. Among the 974 dive depths recorded, 1% were discarded due to biologically implausible depth records when comparing the depth recorded by the tag to the bathymetry for the same location (>100 m). When considering all tracks as a whole, the maximum dive depth ranged from 10 to 100 m, and 70% of the dives were performed at shallow depths within 30 m of the surface (Fig 4A). The depth range was greater outside the foraging areas and ranged from 10 to 100 m, whereas turtles concentrated their dives between 10–30 m at the foraging

Table 1. Summary of the horizontal and vertical movements of the 19 green turtles during the three migration phases. The diving parameters refer only to the 14 Argos-Fastloc GPS tags. The numbers 1, 2 and 3 refer to the three migration phases, respectively before, within and after the plume.

	Migration phase			All migration
	1	2	3	Mean±SD
Distance to shore (km)	13.5±8.4	46.6±45.7	17.3±11.3	22.5±24.4
Observed speed ($m.s^{-1}$)	0.6±0.5	0.8±0.6	0.6±0.5	0.5±0.5
Swimming speed ($m.s^{-1}$)	1.0±0.5	1.1±0.6	0.9±0.5	0.8±0.5
Current velocity ($m.s^{-1}$)	0.5±0.2	0.4±0.3	0.3±0.1	0.4±0.2
Maximum depth (m)	26.6±25.3	38.7±28.8	34.5±18.4	32.0±20.9
Maximum duration (min)	35.2±23.6	29.1±23.4	37.4±22.5	35.1±21.9

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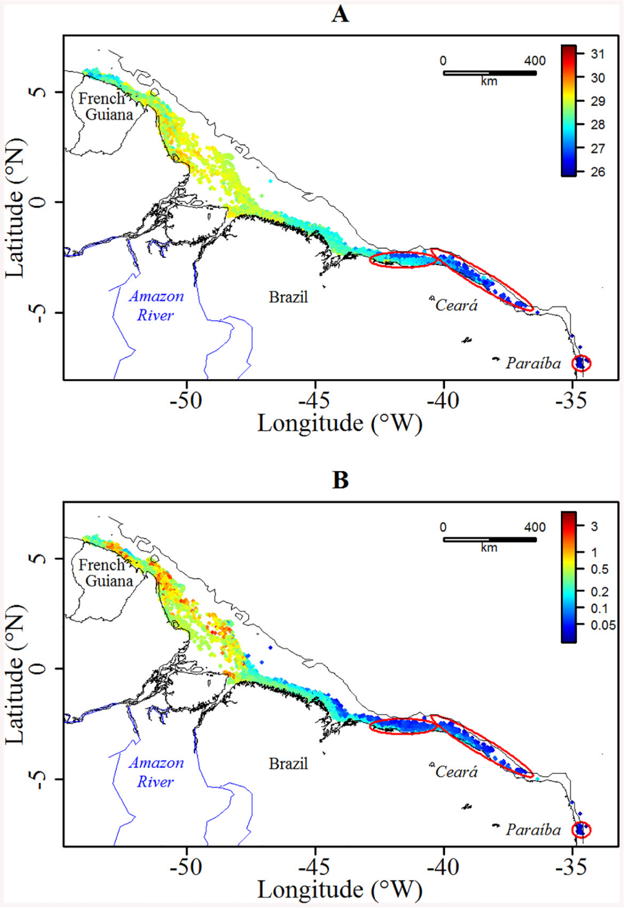

Fig 2. Distributions of (A) SST (°C) and (B) K_d (m^{-1}) along the 19 turtles' tracks. The foraging grounds are represented by the red ellipses and the black solid line refers to the 100 m isobaths. K_d refers to the Diffuse Attenuation Coefficient and was logged transformed for a better contrast. The shoreline was extracted from NOAA National Geophysical Data Center, Coastline.

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grounds. Mean depth was significantly higher outside the foraging areas (Wilcoxon test: $p < 0.001$, 29.5±12 m vs. 33.7±25.1 m)–see Fig 4A.

Regarding the overall distribution of the maximum dive duration, the dives ranged from 0.5 to 70 min and 35% of the dives lasted 30–40 min (Fig 4B). Wherever the foraging area was located, i.e. whether it was off the shores of Cayenne or at the end of the migratory path, dives lasted significantly longer at the foraging grounds (37.3±19.1 min) than during the transiting between feeding sites (33.6±23.5 min, Wilcoxon test: $p < 0.001$).

Behavioral adaptations to environmental conditions

Distance to shore. Over the entire migration, 88% of the locations were located in areas with a north-westward current flowing against the migratory path of the turtles (Fig 5). However, the strongest velocities flow parallel to the coastline at around 100 km offshore, i.e. the North Brazil current, and turtles remained on average within 22.5±24.4 km of the shore (Table 1). Current velocity was positively correlated to the distance to the shore (Spearman correlation test: $R^2 = 0.36$, $p < 0.001$), especially within the plume (Spearman correlation test: $R^2 = 0.57$, $p < 0.001$).

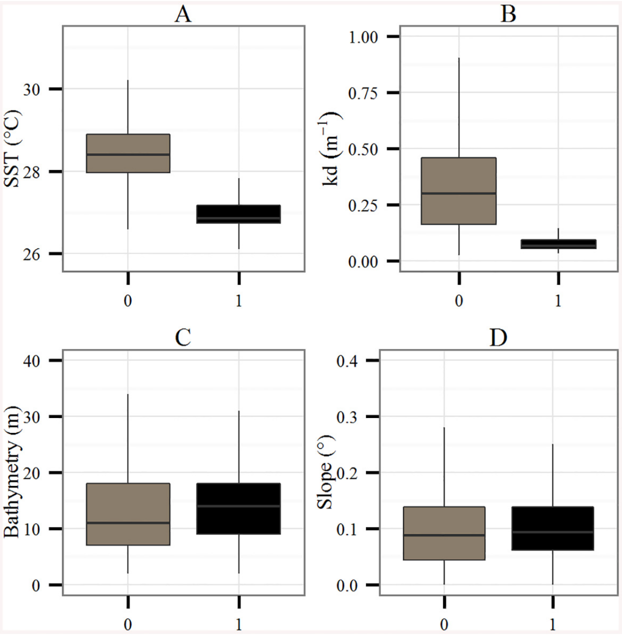

Fig 3. Box plots of (A) the SST (°C), (B) the K_d (m^{-1}), (C) the Bathymetry (m) and (D) the Slope (°) extracted at turtles' locations for the two behavioral modes, i.e. transiting (grey) and foraging (black).

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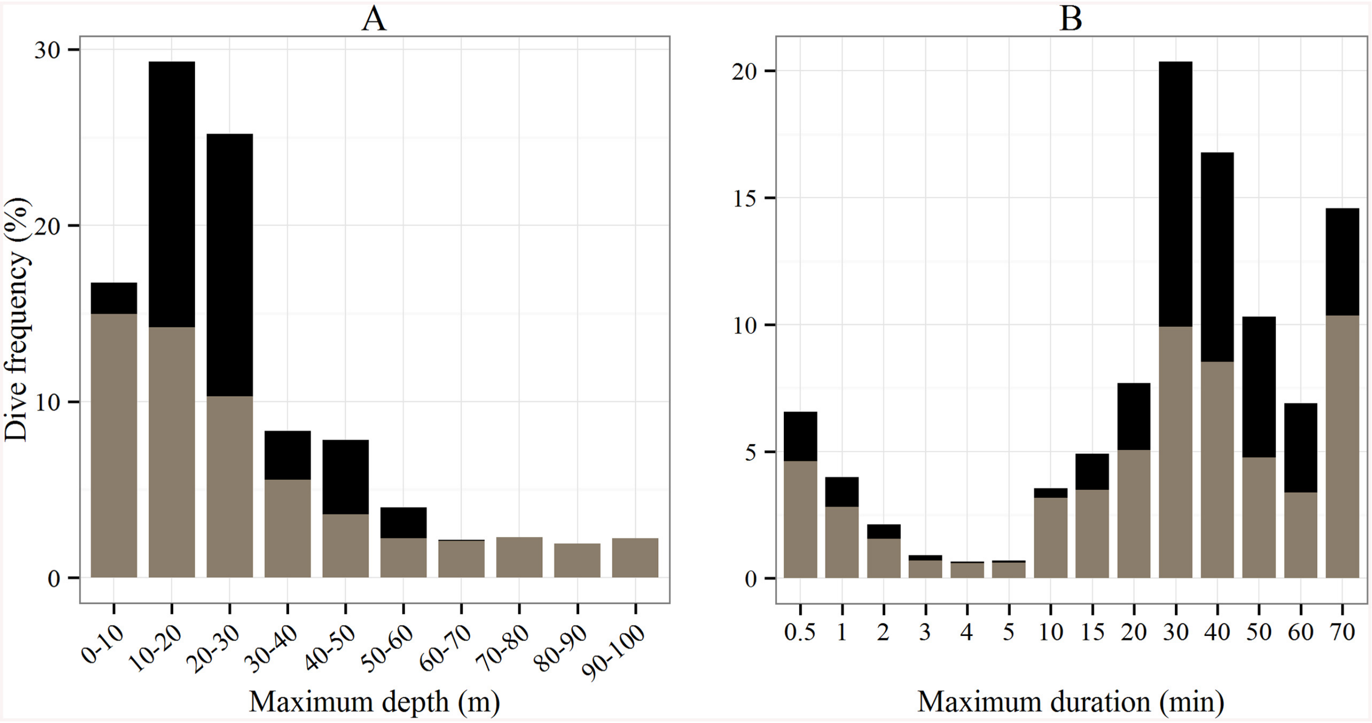

Fig 4. Histograms of (A) the maximum dive depth (m) and (B) the maximum dive duration (min) recorded by the 14 Argos-Fastloc GPS tags for the two behavioral modes, i.e. transiting (gray) and foraging (black).

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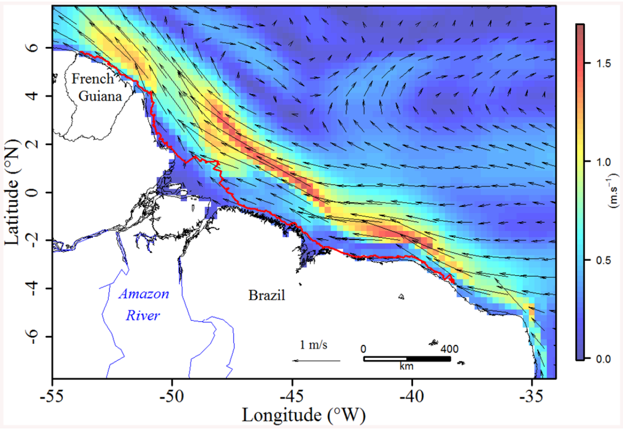

Fig 5. Mean direction and velocity of the currents over the whole study area for the 2012 and 2014 tracking periods extracted daily from Mercator-Ocean GLORYS-2v1 (Global Ocean ReanalYsis and Simulations). The trajectory of turtle #115452 (red) is superimposed on the current. For a better visual representation, the spatial resolution of the current direction is set to 0.75 degrees. The shoreline was extracted from NOAA National Geophysical Data Center, Coastline.

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The distance to shore varied significantly between all migration phases (Tukey HSD: $p < 0.001$, Table 1). Turtles swam closer to shore before and after the mouth of the Amazon (Phases 1 and 3), swimming over twice as far from the coast while crossing the plume (46.6 ±45.7 km) than in any other parts (17.4±11.4 km, Fig 6).

Speed. Except between Phase 1 and Phase 3, the observed speed differed significantly according to the migration phase, and was highest within the plume and lowest before and after the plume (0.8±0.6 $m.s^{-1}$ vs. 0.6±0.5 $m.s^{-1}$, Tukey HSD: $p < 0.01$, Table 1). Over the entire migration, the average swimming speed after correction for currents was higher than the observed speed (0.5±0.5 $m.s^{-1}$ vs. 0.8±0.5 $m.s^{-1}$ ~3 $km.h^{-1}$), with minimum values observed after the plume and maximum values recorded at the Amazon mouth in Phase 2 (0.9±0.5 $m.s^{-1}$

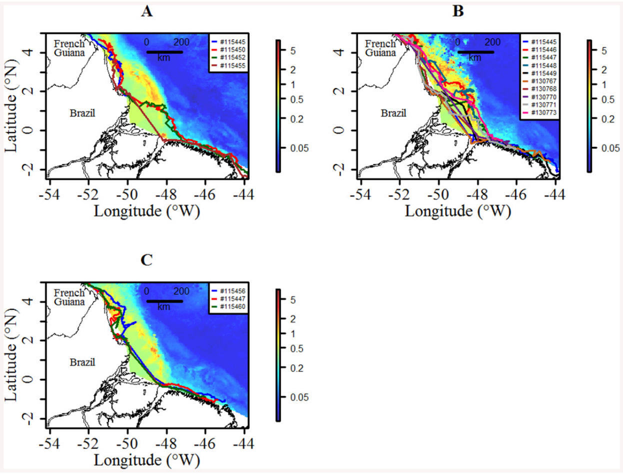

Fig 6. Map of K_d (m^{-1}) within the plume for (A) May, (B) June and (C) July, with turtle routes superimposed for the corresponding months. The K_d was log transformed to improve representation and extracted monthly from Ocean Colour database and the shoreline comes from NOAA National Geophysical Data Center, Coastline.

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vs. 1.1±0.6 m.s^{-1}). There was also a positive relationship between the current velocity and the swimming speed (Spearman correlation test: $R^2 = 0.2$, $p < 0.001$), meaning that turtles increased their swimming effort with the increasing velocity of the oncoming current.

Time spent within the plume. The most parsimonious model associated with the lowest AIC contained two variables: the time taken to reach Foraging Grounds (Time to FG) and the minimum FG longitude (closest foraging ground to the nesting site)–see Table 2. There was no relationship between the time spent in Phase 2 and body mass (Spearman correlation test: $R^2 = 0.04$, $p = 0.8626$), or swimming speed within the plume (Spearman correlation test: $R^2 = 0.31$, $p = 0.2122$). In contrast, Time within the plume increased significantly with the time taken to reach the foraging ground ($p < 0.01$, Table 2), whereas the minimum longitude of foraging grounds decreased significantly with TimePhase2 ($p < 0.001$, Table 2).

Diving behavior. Mean depth was significantly different between all migration phases (Tukey HSD: $p < 0.001$, Fig 7A), and on average, turtles dived deeper in Phase 2 and to shallower depths in Phase 1 (39.2±21.8 m vs. 26.6±25.3 m, Table 1). Maximum dive duration varied significantly between all migration phases except between Phase 1 and Phase 3 (Tukey HSD: $p < 0.001$, Fig 7B). The longest average dive duration was performed in Phase 3 (37.4 ±22.5 min), whilst the shortest occurred in Phase 2 (29.1±23.4 min).

Discussion

Our study uses satellite telemetry and two years of sampling (2012 and 2014) to provide data highlighting the long, counter-current post-nesting migration performed by green turtle *Chelonia mydas* population nesting in French Guiana and Suriname, and reveals a substantial foraging aggregation off the Brazilian coast. The assessment of their spatial and diving patterns in response to environmental variability, i.e. the North Brazil current and the Amazon River plume, provides detailed information on their behavioral adjustments and specific habitat affinities.

Synchronization and foraging aggregation

A previous study tracked green turtle individuals from the closest rookery to French Guiana, located on the beaches of Tortuguero in Costa Rica [44]. Although there are similarities with our group in terms of coastal migration and proximity to foraging grounds, green turtles from French Guiana and Suriname travelled on average more than three times the maximum distance travelled by the Tortuguero individuals (3681±729 km vs. 1089 km) [44]. Additionally, one individual nesting in French Guiana travelled the longest total distance ever recorded for a green turtle, i.e. 5153 km. This difference in coastal migration distances between the two green turtle populations is striking. Although long travel distances have already been documented for turtles that nest on isolated islands and therefore have to cross the open ocean or the open seas [45,46], they have never been observed before in green turtles migrating exclusively alongshore.

Table 2. Summary of the linear model performed to relate the *TimePhase2 to intrinsic variables.**

Variable	Estimate	Std error	Z value	p-value
Time to FG	4.2361	1.5980	2.651	<0.01
Min Longitude FG	-4.9891	1.5980	-3.122	<0.001

TimePhase2* refers to the time (in days) spent within the plume and FG to Foraging Grounds.

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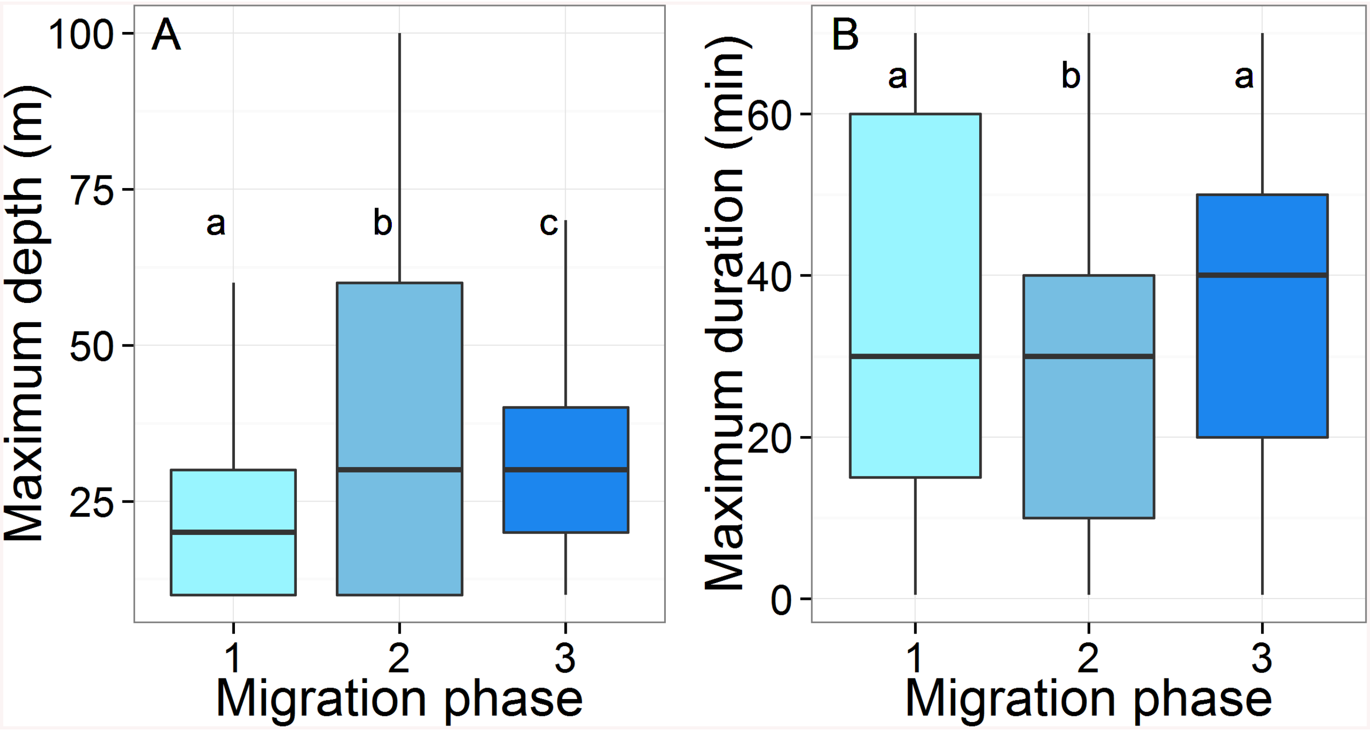

Fig 7. Box plots of (A) the maximum depth (m) and (B) the maximum duration (min) recorded by the 14 Argos-Fastloc GPS tags during the three migration phases. The box plots sharing the same letter are not statistically different (Tukey HDS). The horizontal black line in box plots represents the median.

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Unlike green turtles in Costa Rica, which displayed migration routes that differed according to individuals [44], the 19 turtles in our study exhibited a remarkable synchronization in time and space since they all travelled in the same direction and during the same period. With the exception of one individual performing a foraging behavior off Cayenne (#115446), the 18 others performed a remarkably straight course to their final destination, and did so within a quite limited time. This pattern suggests an optimal strategy which involves minimizing the cost of migration for turtles by allowing the rapid restoration of their body reserves after the inter-nesting season [45]. The single foraging event located off Cayenne does not correspond to the presence of seagrass beds, and can be attributed to either navigational issues caused by hydrodynamic forcing (this turtle swam in two uniform anticlockwise circles, suggesting that the North Brazil current and/or the north-westward Amazon plume pushed her back in the opposite direction), or a stopover site as identified by Baudouin et al. [21], since this individual could have let itself drift passively in this stopover area.

Suitable habitat for a mega-herbivore reptile

Our data show that the most favorable habitat conditions for the foraging activity of green turtles are clear and cool waters, which are associated with low bathymetry. Data on seagrass coverage confirms that green turtle foraging grounds are located near seagrass beds. Seagrass is a fragile ecosystem relying on complex biochemical processes, since its growth is regulated by temperature, light and nutrient availability [47,48]. However, the 115.10^7 tons/year of sediments discharged by the Amazon River plume strongly influence the optical conditions of the north-eastern American coast [24,26], leading to large amounts of suspended and dissolved materials [27] that limit underwater irradiance [47,49]. These unfavorable conditions for seagrass growth may explain why green turtles cross the plume at high travel speeds, i.e. to reach the clearer waters further south that are associated with seagrass meadows. The presence of seagrass beds at green turtle foraging grounds is also noted in the observations of the Federal University of Rio Grande (FURG) [22]. Indeed, five seagrass species have been identified along the tropical coast of Brazil from 0 to 25°S [22]. These species extend over > 30 000 ha, namely *Halodule wrightii*, *H. emarginata*, *H. decipiens*, *H. bailoni* and *Ruppia maritima*. *H. wrightii* seems to be the dominant species within green turtle foraging grounds. The biomass of this seagrass species is greater during spring and summer compared to fall and winter [50], which corresponds to the arrival time of green turtles and suggests that the migration timing of this grazer matches the seasonal abundance of seagrass [1].

Ceará was described as a foraging ground for green turtles of the Equatorial Atlantic in the 1970s, when several individuals from French Guiana were observed off the Brazilian coast [51]. Further evidence was seen in 2001 and 2003, when green turtles tagged in Brazil were recaptured in Nicaragua (data available on www.seaturtle.org). Other observations provide links between Ceará foraging grounds and other nesting sites in the tropical Atlantic, such as the Caribbean region and Central America. Furthermore, green turtles nesting on Ascension Island migrate to foraging grounds off Paraíba state [51,52], a site reached by one of the individuals in our study (#115460).

The turtles performed longer dives in foraging areas, which strongly suggests the occurrence of feeding activity [10,44]. The difference in water temperature within the plume and inside foraging grounds (~1.9°C) can be explained by the warmer freshwater supply from the Amazon River [53]. Cooler temperatures in foraging areas may therefore play two roles: firstly they favor seagrass development under optimal conditions [48], and secondly they allow these ectothermic organisms to reduce their metabolism and thus minimize their energy expenditure [54]. A reduced metabolic rate may therefore enable turtles to dive for longer periods, optimizing resource exploitation [55].

Dispersal adaptations to counterbalance the effect of strong currents

The migration trajectories of these 19 green turtles highlight a counter-current migration, with inter-individual variability observed for the distance to shore and vertical movements. The surface current velocities show that turtles swim against the current throughout their migration to foraging grounds, which could require high amounts of energy. All individuals travelled at high speeds to compensate for current-induced drift, and approached the speeds reached by green turtles crossing the Atlantic Ocean from Ascension Island (0.56 $m.s^{-1}$ vs. 0.71 $m.s^{-1}$) [21]. However, no documentation to date describes the swimming speed of green turtles after correction for currents. This study provides the first reliable data ever recorded for swimming speeds, and reveals that individuals reached on average 0.84 $m.s^{-1}$, with bursts of speed attaining 3.50 $m.s^{-1}$. It is important to note that higher swimming speeds were recorded at the beginning of the migration, where the current velocities are the strongest, i.e. the Guiana current. Consequently, green turtles could either increase their swimming speed in response to current velocity, i.e. an increase of 46% compared to the initial observed speed, or simply travel faster before the plume because they have more energy at the beginning of the migration than at the end of their journey, thousands of kilometers away.

The North Brazil current carries upper-ocean waters northwards to the Equator with a maximum transport of up to 36 Sv (Sv = 10^6 m^3 s^{-1}) at depths of over 600 m [56]. By keeping their trajectories confined close to the shore, i.e. within an average 23 km from the coastline, turtles show a strategy to save energy by avoiding the strong North Brazil current, which flows at its highest velocities at around 100 km offshore. Furthermore, the post-nesting migration of green turtles spans from April to September; this period coincides with the velocity peak of the North Brazil current, which is at its highest from July to August [56]. Despite the great speed of the North Brazil current, turtles may also be affected by tidal processes as they are travelling very close to the shore. Over the French Guiana continental shelf, tidal currents therefore influence the inner shelf, within 15–20 km from the coastline [57]. During flood of spring tides, tidal currents are directed to the coast, and thus influence the total currents, reaching up to 0.45 $m.s^{-1}$ [57]. The alongshore current can therefore be turned into a cross-shore current, that favor turtles displacements. Decreasing bathymetry combined with bottom friction may also play a significant role in coastal current dissipation alongshore [58,59], explaining why turtles keep their trajectories close to the shore before and after the plume, saving energy during migration. In addition, the first individuals to leave the nesting site in April probably avoided the peak strength of the North Brazil current, giving them the opportunity to reach their foraging grounds rapidly and begin their foraging activity further south. In contrast, turtles would face higher energy requirements when migrating at the end of the season, i.e. when the currents are at their strongest at the end of May or even during June.

Behavioral adjustments to cross the Amazon River plume

The significant increase in distance to shore for all individuals when crossing the plume indicates that the green turtles also adapted their behavior to the Amazon River plume. Two different spatial patterns appeared: some individuals remained close to shore during the plume crossing, whereas others swam farther from the shore, i.e. up to 200 km offshore. The latter spent more time in the plume phase due to the higher current velocity at greater distances from the coastline. This suggests that travelling alongshore when crossing the plume is probably the optimal dispersal strategy to avoid the strong North Brazil current and reach the foraging grounds more rapidly for body reserve repletion. However, turtles could also cross the mouth of the Amazon further out to sea, either to avoid the high current velocity of the plume, or, more probably, to reduce the distance travelled by choosing the shortest path to reach the foraging grounds instead of following the coastline [10].

Although the strength of the plume appears to be relatively stable across the years, the Amazon River plume shows a notable seasonal variability [53,60,61], with river discharges that attain maximum levels of approximately 2.4×10^5 m^3 s^{-1} between May and June [53]. This variability could lead to the selection of different foraging areas within the breeding seasons, with a potential lack of site fidelity among individuals. Indeed, unlike the green turtles of the Mediterranean sea, which use similar migratory routes to reach the same foraging grounds from one year to the next [62], green turtles in the Equatorial Atlantic may use different foraging areas off the Brazilian coast throughout the breeding seasons, depending on the date migration begins. Indeed, the interannual variability of the number of clutches laid and the variable remigration interval (from 2 to 3 years) observed in green turtles of the Mediterranean Sea [63] could potentially affect the duration of the inter-nesting season, and consequently the month migration starts. In turn, it might define the month during which turtles might cross the river plume. It would therefore be interesting in a future study to tag the same individuals to compare their different post-nesting migration routes and assess site fidelity.

Crossing this physical barrier may alter the rest of the migration, and consequently affect the choice of foraging ground location and the time required to reach foraging grounds. Our data show that the longer individuals stayed within the plume, the sooner they initiated foraging on seagrass beds, suggesting that the crossing of the highly turbulent plume resulted in higher energy expenditure. In contrast, turtles that crossed the plume at a higher speed stopped further south, where seagrass beds tend to be of higher quality and are more abundant. The date of departure was an important factor, as the first individuals to leave the nesting site crossed the plume more rapidly. Indeed, given that the velocity peak of the Amazon plume is reached in May-June, individuals that left French Guiana early in the inter-nesting season, i.e. in April or beginning of May probably avoided the peak of water discharges, therefore limiting their energy expenditure. Nevertheless, whatever the time spent within the plume, travel speed was higher for all individuals within the plume, confirming the need to cross this unfavorable area (without seagrass or visibility) as fast as possible, as there is no possibility to feed en-route [10]. After the plume, the reduced travel speeds associated with two different stopover areas identified by Baudouin et al. [21] reinforce the assumption that individuals would need to recover after crossing such a turbulent zone.

Diving behavior might also change during migration in an effort to adapt to various abiotic conditions. Simulations of the Amazon River discharge have demonstrated a weak return current in the underlying seawater beneath the surface and a reduction of the plume velocity in deeper layers [53]. Since the plume is 3–10 m deep [61], individuals could avoid the strong current and turbid surface layer by targeting specific depths beyond 10 m. This could be confirmed by retrieving the tags and downloading the high resolution data that were not transmitted. The shorter dives within the plume highlight the energetic costs involved in crossing such a turbulent area, and could be a means to avoid being swept seaward by the Amazon flow. Short dives could also enable green turtles to return to the surface more frequently, as they may use airborne odorants associated with land to maintain their course in the highly turbid waters of the plume. This theory was demonstrated in loggerhead turtles [64] and could be an additional orientation cue used by green turtles nesting in French Guiana during their migration. It would be interesting to deploy acceleration data loggers in a further study to determine the relationships between energetic expenditure and environmental variables and investigate whether green turtles feed en-route before reaching their foraging grounds [65,66].

Conclusions and Perspectives

Our data provide detailed information on the habitat requirements for one of the two main activities occurring in the life cycle of adult green turtles, i.e. post-nesting migration to foraging areas. This study highlights several behavioral adjustments in both horizontal and vertical movements in response to a highly dynamic zone under the influence of the North Brazil Current and the Amazon River plume. Unlike green turtles from Ascension Island, which use the South Atlantic equatorial current during their post-nesting migration [67], green turtles from French Guiana seem to perform the opposite strategy and swim against the currents during their post-nesting migration. The deployment of tags on females at the foraging grounds in Brazil, before their return journey to French Guiana, would be an opportunity to investigate the potential use of the North Brazil current by green turtles on their return trip to optimize the energy stores they have gained at the foraging grounds. Contrary to the pattern seen over their migration towards the foraging grounds, turtles might therefore migrate farther from the coast on their return journey in order to take advantage of stronger currents.

Supporting Information

S1 Fig. a) Variances of the FPT according to the ARS spatial scale (*r* in km) for each individual. The red dotted lines and the bold numbers indicate the radii referring to the highest FPT variances. **b) FPT (in days) over time for the optimum radii of each individual**. The red lines indicate Lavielle segmentation corresponding to the ARS events.
(DOCX)

S2 Fig. Monthly K_d distributions (in m^{-1}) over the whole study area extracted daily from Mercator-Ocean GLORYS-2v1 (Global Ocean ReanalYsis and Simulations) in (A) April, (B) May, (C) June, (D) July, (E) August, (F) September and (G) October. The shoreline was extracted from NOAA National Geophysical Data Center, Coastline.
(DOCX)

S1 Table. Summary of the horizontal movements of the 19 individuals over the entire tracking period. Nloc refers to the total number of positions recorded per individual.
(DOCX)

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Author Contributions

Conceived and designed the experiments: DC. Performed the experiments: DC. Analyzed the data: PC. Contributed reagents/materials/analysis tools: DP VV PG BT DC. Wrote the paper: PC DP VV LK ME CG RB KB PG YLM.

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ANNEXE F

The influence of oceanographic features on the foraging behavior of the olive ridley sea turtle *Lepidochelys olivacea* along the Guiana coast

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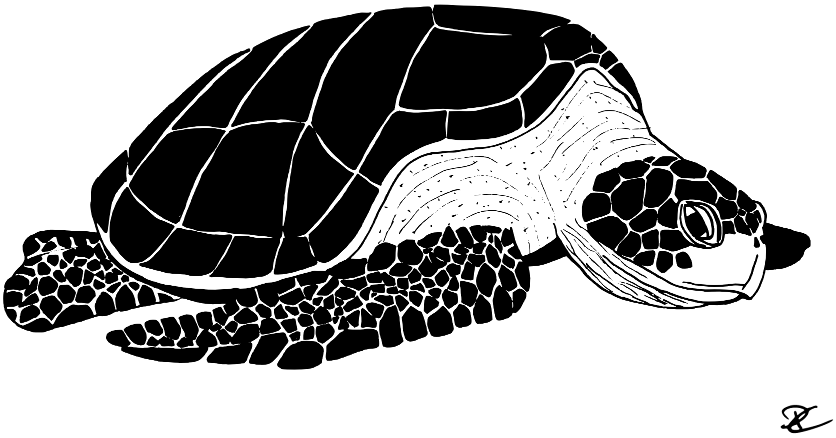

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The influence of oceanographic features on the foraging behavior of the olive ridley sea turtle *Lepidochelys olivacea* along the Guiana coast

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ABSTRACT

The circulation in the Western Equatorial Atlantic is characterized by a highly dynamic mesoscale activity that shapes the Guiana continental shelf. Olive ridley sea turtles (*Lepidochelys olivacea*) nesting in French Guiana cross this turbulent environment during their post-nesting migration. We studied how oceanographic and biological conditions drove the foraging behavior of 18 adult females, using satellite telemetry, remote sensing data (sea surface temperature, sea surface height, current velocity and euphotic depth), simulations of micronekton biomass (pelagic organisms) and *in situ* records (water temperature and salinity). The occurrence of foraging events throughout migration was located using Residence Time analysis, while an innovative proxy of the hunting time within a dive was used to identify and quantify foraging events during dives. Olive ridleys migrated northwestwards using the Guiana current and remained on the continental shelf at the edge of eddies formed by the North Brazil retroflection, an area characterized by low turbulence and high micronekton biomass. They performed mainly pelagic dives, hunting for an average 77% of their time. Hunting time within a dive increased with shallower euphotic depth and with lower water temperatures, and mean hunting depth increased with deeper thermocline. This is the first study to quantify foraging activity within dives in olive ridleys, and reveals the crucial role played by the thermocline on the foraging behavior of this carnivorous species. This study also provides novel and detailed data describing how turtles actively use oceanographic structures during post-nesting migration.

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1. Introduction

The circulation in the Western Equatorial Atlantic is characterized by a highly dynamic mesoscale activity driven by the North Brazil Current (NBC) and the North Equatorial Countercurrent (NECC) (Pauluhn and Chao, 1999; Froidefond et al., 2002; Fratantoni and Richardson, 2006) – see Appendix A. The NBC originates from the South Equatorial Current, and carries upper-ocean waters northwards to the equator. During the boreal fall season, a large part of the NBC at approximately 7°N–48°W retroflects eastwards, feeding the NECC (Lumpkin and Garzoli, 2005). This retroflection generates anticyclonic eddies with radii up to 200 km, which then move toward the Caribbean for several months every year (Didden and Schott, 1993).

These mesoscale features transport and disperse nutrient-rich waters originating from the Amazon River, further east (Baklouti et al., 2007). The Amazon is the largest river in the world, and discharges large amounts of sediment as well as particulates and chromophoric dissolved organic materials ($115 \cdot 10^7$ tons per year) into the Equatorial Atlantic Ocean (DeMaster et al., 1996; Meade, 1996). In this context, the Amazon plume strongly influences the oceanographic and biochemical conditions in the north-eastern part of the South American continental shelf, stretching from the

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North Brazilian coast to the Caribbean, making it a highly productive area (Muller-Karger et al., 1988; DeMaster et al., 1996).

The French Guiana continental shelf reaches from the Amazon River to the Trinidad Island sector and hosts three sea turtles species, namely the green turtle *Chelonia mydas* (Baudouin et al., 2015; Chambault et al., 2015), the leatherback *Dermochelys coriacea* (Fossette et al., 2006, 2010a,b) and the olive ridley *Lepidochelys olivacea* (Kelle et al., 2009; Plot et al., 2015). Although all three species remain on the continental shelf throughout the breeding and nesting seasons (Fossette et al., 2006; Georges et al., 2007), they exhibit different dispersal strategies during their post-nesting migration (Fossette et al., 2010b; Chambault et al., 2015; Plot et al., 2015; Baudouin et al., 2015). Only the olive riley sea turtles remain on the French Guiana continental shelf after the nesting season (Plot et al., 2015).

The olive ridley population that nests in French Guiana remains within the neritic domain during its northwestward post-nesting migration, which is an unusual habitat, confirming that this species can occupy different habitats according to the population (Polovina et al., 2004). Olive ridleys also exhibit behavioral plasticity in terms of dispersal and diving behavior through the use of different habitats according to the individual, i.e. the continental shelf, the continental slope or deep waters (Plot et al., 2015). This post-nesting migration, over the Guiana basin, occurs in the equatorial waters of the Atlantic, making this site unique as it is on the very periphery of the species range (Grinnell, 1917). Furthermore, nothing is known to date about how this population uses mesoscale features to forage at its range boundaries.

This study is the first to investigate the role of mesoscale features in the foraging behavior of olive ridley sea turtles. Mesoscale features such as eddies, fronts and upwelling/downwelling are highly variable in size and duration, covering from 100 km to 500 km and lasting anywhere between 10 and 100 days (Croxall, 1987). They are expected to strongly influence the foraging strategies of pelagic organisms, especially marine megafauna (Bailleul et al., 2010). Indeed, these oceanic structures contribute to ocean mixing, enhancing primary productivity at low trophic levels and concentrating prey for megafauna organisms, thereby affecting the entire food chain through bottom-up processes (Lévy, 2008). Recent studies in two different populations of elephant seals have demonstrated links between foraging behavior and eddies – fronts (Campagna et al., 2006; Bailleul et al., 2010; Dragon et al., 2010). Similar results have been obtained in cetaceans (Davis et al., 2002), seabirds (Weimerskirch et al., 2004; Pinaud and Weimerskirch, 2005; Cotté et al., 2007; Tew-Kai and Marsac, 2009) and sea turtles (Polovina et al., 2006; Lambardi et al., 2008), indicating that areas of high productivity provide feeding grounds for a broad range of marine megafauna species.

To date, the identification of eddies and fronts has mainly been based on remote sensing data such as Sea Surface Temperature (SST), Sea Surface Height (SSH), primary production and oceanic circulation (current velocity). However, an innovative modeling approach based on the distribution of pelagic preys has emerged over the last decade: the Spatial Ecosystem And Population Dynamics Model (SEAPODYM) (Lehodey et al., 2008). This model of mid-trophic organisms is based on several types of prey that are vertically distributed within the water column, i.e. the micronekton. The technique has been initially used to predict tuna population dynamics (Lehodey et al., 2010a,b; Lehodey et al., 2012; Sibert et al., 2012) and recently cetacean distribution (Lambert et al., 2014), and also to simulate turtle movements (Abecassis et al., 2013).

Several techniques have been developed to detect foraging events. In the horizontal dimension, the identification of Areas of Restricted Search (ARS) was based on the detection of decrease in travel speed and increase in turning angles (Kareiva and Odell, 1987; Robinson et al., 2007; Dragon et al., 2012). The detection of ARS has helped to identify foraging activity in numerous species via a wide range of techniques (Fauchald and Tveraa, 2003; Weimerskirch et al., 2004; Jonsen et al., 2005, 2006, 2007; Gaspar et al., 2006; Pinaud, 2008; Bailey et al., 2008; Barraquand and Benhamou, 2008; Dragon et al., 2012; Plot et al., 2015). There is a significant depth structure to foraging behavior within the water column in particular areas of prey aggregation (Fuiman et al., 2002; Watanabe et al., 2003; Mitani et al., 2003), making it essential to take the vertical dimension into account as well (Bailleul et al., 2008). New techniques using acceleration data from data loggers placed on pinnipeds (Viviant et al., 2014; Labrousse et al., 2015) and sea turtles (Okuyama et al., 2009; Fossette et al., 2010a,b, 2012a,b) have made it possible to identify prey capture attempts during the dives. However, such techniques were mostly inapplicable to low resolution datasets, which require tag retrieval after tracking (Heerah et al., 2014, 2015). Consequently, vertical foraging activity is often identified and quantified using foraging indices such as bottom time, dive shape (Fedak et al., 2001; Dragon et al., 2012) or, more recently, hunting time (Heerah et al., 2015). This study applies the hunting time index to olive ridley sea turtles for the first time, making it possible to estimate the time spent foraging within-dives.

In 2013 and 2014, satellite tags were deployed on 20 adult female olive ridley sea turtles to assess the influence of oceanographic and biological features on their foraging behavior in horizontal and vertical dimensions during their post-nesting migration from French Guiana. This study aims to (1) analyze horizontal movements in relation to remote sensing data and micronekton biomass, then to (2) quantify and link foraging events within dives to *in situ* data directly recorded within the water column.

2. Materials and methods

2.1. Ethics statements

This study met the legal requirements of the country in which the work was carried out, and followed all institutional guidelines. The protocol was approved by the "Conseil National de la Protection de la Nature" (CNPN, http://www.conservation-nature.fr/acteurs2.php?id=11), which is under the authority of the French Ministry for ecology, sustainable development and energy (permit number: 09/618), and acts as the ethics committee for French Guiana. The fieldwork was carried out in strict accordance with the recommendations of the Police Prefecture of Cayenne, French Guiana, France, in order to minimize any disturbance of the animals.

2.2. Study area and tag deployment

During the 2013 and 2014 nesting seasons, 20 adult female olive ridleys were equipped with satellite tags on the beaches of Remire-Montjoly (4.53°N–52.16°W, Cayenne, French Guiana). Eight Argos-linked Fastloc GPS tags (MK10, Wildlife Computers Redmond, WA, USA) were deployed from July to August 2013. Twelve Conductivity Temperature Depth Fluorometer-Satellite Relayed Data Loggers (CTD-SRDL, Sea Mammal Research Unit, University of St. Andrews, Scotland) were fitted during the same period in 2013 ($n = 2$) and 2014 ($n = 10$).

Using a red light to minimize disturbance, the satellite tags were attached during night-time egg laying, i.e. at the only moment when individuals are static – for details see Baudouin et al., 2015. The carapace was cleaned with scrapers, water and acetone, then the tags were fixed to the carapace as close as possible to the head using an epoxy resin, with the antenna facing forward. To allow the resin to dry completely, turtles were then herded into a pen for approximately 2 h before being released. During tag deployment, measurements of the Curved Carapace Length (CCL) were also taken.

2.3. Data collected from the tags

The procedure for data extraction of the migratory routes is described in Baudouin et al. (2015). Diving behavior data recorded by the tags describe specific diving parameters, namely maximum dive depths and dive durations and *in situ* temperature data, binned as 4-h period histograms. Maximum depths were collected in different bins, every 10 m from 10 to 100 m, then every 50 m from 100 to 250 m. Similarly, maximum dive durations were stored from 30 s to 1 min, then every minute from 1 to 5 min, and finally every 10 min from 10 to 60 min. *In situ* temperatures from 20 to 32 °C were recorded during dives with a resolution of one degree Celsius. Tags also supplied Time At Depth (TAD) and Time At Temperature (TAT), defined as the proportion of time (in %) spent at each depth and the temperature range, respectively.

The 12 CTD-SRDL tags provided the locations of turtles via the Argos Doppler Location algorithm (Lopez et al., 2014), data on diving behavior including dive depth, dive duration, time at depth and duration of post-dive surface intervals, and oceanographic data in the form of vertical temperature and salinity profiles taken during the ascent phase of turtle dives (Boehme et al., 2009). The CTD-SRDL tags were programmed to send summarized dive profiles using the compression algorithm described by Fedak et al. (2001) with four depth records for each dive (instead of 1 maximum depth per dive for the Argos-Fastloc GPS tags). Temperature and salinity data were quality controlled using the procedure described in Roquet et al. (2011), with an estimated accuracy of 0.02 °C in temperature and 0.05 in salinity. Similar CTD-SRDL tags have been extensively used on seals in polar regions over the last decade, and particularly in the Southern Ocean, where they have become a major source of oceanographic data (Roquet et al., 2013). To our knowledge, our study is the first to use CTD-SRDL tags to study sea turtles in a tropical region.

2.4. Data pre-filtering

As the tags were deployed during the nesting season, they recorded both the nesting and migration phases. We therefore performed a spatial query via ArcGIS version 10.1 to identify the date of migration departure based on the distance traveled from the nesting site and the last nesting event (identified thanks to the wet/dry sensor of the tag) to exclude the nesting period from our data, thus ensuring that the migration phase alone was retained in the analysis (Baudouin et al., 2015). A Kalman filtering algorithm was then applied to the locations (CLS, Collecte Localisation Satellites, Toulouse, France) to enhance tag position estimates (Argos and GPS) (Silva et al., 2014). The General Bathymetric Chart of the Oceans (GEBCO) database (http://www.gebco.net/, resolution 30 arc-sec, ~1 km grid) was used to discard any locations on land. The Argos Kalman-filtered locations associated with a swimming speed of over 10 km h^{-1} were also discarded, as well as any locations classed as Z, considered insufficiently accurate.

2.5. Identification of foraging grounds in the horizontal dimension

ARS were identified by applying a two-step procedure to the location data (Argos and GPS of both tag instruments), namely (1) First Passage Time (FPT) analysis (Fauchald and Tveraa, 2003) followed by (2) Residence Time (RT) analysis (Barraquand and Benhamou, 2008). FPT is defined as the time required by an organism to cross a circle of a given radius. The optimal ARS circle radius for each turtle was estimated using the *fpt* function from the *adehabitatLT* package from the R software version 3.1.2 (R Core Team, 2014). Tested radii ranged from 1 to 400 km to ensure the coverage of large foraging movements (Fauchald and Tveraa, 2006). For each track, the relative variance of FPT (log transformed) was plotted against radii to identify the different scales of the searching activity (ARS radius) revealed by a peak of variance at a specific radius. After identifying the optimal ARS scale for each individual, RT analysis was performed on the data to distinguish between the 'transiting' mode (low RT) and the 'foraging' mode (high RT) in both time and space. This was achieved through the temporal detection of ARS periods using Lavielle's segmentation method (2005) from the *adehabitatLT* package (Calenge, 2006).

2.6. Relating horizontal foraging activity to surface biological variables

We related the foraging activity of olive ridleys to the distribution of their prey using the SEAPODYM model, (Lehodey et al., 2010a). SEAPODYM predicts the spatio-temporal distribution of micronekton, the smallest pelagic organisms able to swim against sea currents (individuals measuring from 2 to 25 cm). This model creates an idealized 3-layer ocean simulation, and organisms are classified into six functional groups according to their diel vertical migration behavior (Lehodey et al., 2010a,b).

SEAPODYM takes the carnivorous diet of olive ridleys into account, and encompasses different potential preys including cephalopods, jellyfishes, crustaceans and fishes (Brodeur et al., 2005). The SEAPODYM simulation takes oceanographic components such as currents, temperature, primary production and euphotic depth into consideration and provides micronekton biomass and production on a regular grid of 0.25° at a weekly resolution. As olive ridleys remain mainly above depths of 80 m, we only considered the first SEAPODYM layer. Groups were split into night and day distributions, e.g. MNKnight and MNKday.

2.7. Relating horizontal foraging activity to surface oceanographic variables

We calculated the total distance traveled and the tracking duration using the *trackDistance* function from the *trip* package (Luque, 2007), then derived the travel speed from this data. To investigate the role of oceanic circulation on turtle movements, surface current data (meridional and zonal components) were extracted daily from the Operational Mercator Global Ocean analysis and forecast system, at a resolution of 0.08° (~9 km) (data available on: http://www.myocean.eu/). Oceanic current velocity and direction were then derived from meridional and zonal components (scalars u and v, respectively). Turtle swimming speed was then calculated with a correction for current velocity to give a proxy of swimming effort (Gaspar et al., 2006; Cotté et al., 2007).

To describe the habitat of olive ridleys at their foraging grounds, we used the daily data of two additional oceanographic variables extracted from the Mercator Ocean model at a spatial resolution of 0.08°: SSH, as an indication of mesoscale activity (Stammer and Wunsch, 1999) and SST, influencing the metabolism of turtles and prey distribution. Sea Surface Salinity was not included because the strong influence of the Amazon River can lead to a bias in the estimation of variables in this region and because other river outputs along the Guiana basin are not taken into account by Mercator.

All the values of these three dynamic variables were then extracted at the locations of each turtle using the *extract.data* function from *SDMTools* package (VanDerWal et al., 2014). Bathymetry, a static covariate, was also extracted from GEBCO at each location.

2.8. Identification of foraging activity in the vertical dimension

We discriminated between benthic and pelagic dives by calculating the difference between the bathymetry at the dive location and the maximum dive depth recorded by the CTD-SRDL for the same location for each dive. Therefore, dives with a maximum depth within 3 m of seabed were classified as benthic dives, and those with a maximum depth beyond 3 m from seabed were pelagic dives. The Argos-linked Fastloc GPS tags ($n = 8$) were not incorporated due to the coarser resolution (1 dive depth every 10 m). At some locations, this depth difference was greater than the bathymetry depth, possibly due to the error generated by the shift between the bad Argos positions and the considerable displacements of the turtle during the dive, caused by variable seabed bathymetry. To get an indication of the shape of the dives, we calculated the Time of Allocation at Depth (TAD) index by using the four inflection points of the summarized profiles provided by the CTD-SRDL tags. Based on Fedak et al.'s method (2001), the TAD was calculated in order to give relevant information about where turtles center their activity within the dives, i.e. V-shaped dives for $0.5 \leqslant \text{TAD} < 0.75$ (exploratory dives) and U-shaped dives for $0.75 \leqslant \text{TAD} < 1$ (foraging activity centered at the bottom of the dive). Following the method of Plot et al. (2015), the average rate of change of depth was fixed at 1.4 m s^{-1}.

After identifying the foraging events in the horizontal dimension, we aimed to quantify the vertical foraging activity within a dive. Prey acquisition in marine megafauna is often assumed to occur during the bottom phase of dives (Houston and Carbone, 1992). However, depending on the species and the structure of the oceanographic environment (which ultimately affects prey distribution in the water column), foraging activity can also occur outside the bottom phase, revealing generalist feeding and opportunistic behavior (Heerah et al., 2014). To estimate the foraging activity within a dive, we used a method that was previously applied for Weddel and elephant seals (Heerah et al., 2014, 2015), and which calculates a foraging index, i.e. the hunting time. This method relies on the detection of the vertical ARS, indicated by an increase in vertical sinuosity and a decrease in vertical speed (Heerah et al., 2014). The authors demonstrated that "hunting" phases, i.e. vertical ARS phases, were associated with more prey capture attempts in both high and low resolution dives (Heerah et al., 2014, 2015). Since vertical sinuosity cannot be calculated for low resolution data (only four dive records per dive), Heerah et al. (2015) determined a low-resolution foraging index (hunting$_{\text{lowres}}$ time) based on the detection of reduced vertical speed, i.e. the rate of change between depth segments within a CTD-SRDL dive. Dive segments associated with a vertical speed below a defined threshold (Heerah et al., 2015) are classified as "hunting" whereas segments associated with a greater vertical speed are considered as "transit". The time spent in hunting segments is then added together for each dive to calculate the total hunting$_{\text{lowres}}$ time.

We adapted this approach to olive ridley low resolution datasets by using the density of the vertical speed to test for several hunting time thresholds, and consequently discriminate between transiting vs. foraging modes. Hunting time was calculated for different thresholds of vertical velocity: from 0.01 to 0.5 m s^{-1}, every 0.1 m s^{-1}. For a series of random dives, a visual exploration of the identified hunting vs. transiting mode was performed to identify the correct threshold. A threshold of 0.04 m s^{-1} appeared as the optimal value to discriminate between the two modes. Once the total hunting time had been calculated for each dive, the associated mean depth was extracted, and the hunting time frequency (in %) was derived from the duration of each dive.

2.9. Relating vertical foraging activity to oceanographic variables of the water column

We used the CTD datasets collected from the tags to associate a temperature and salinity value to each mean hunting depth. However, diving and CTD data were stored in separate datasets that rarely matched in time and space, so we searched for the closest CTD profile in time and space for each dive (time window <48 h and space constraint <30 km, i.e. mean daily distance traveled and lowest resolution of the environmental variables extracted). We also identified the thermocline depth (effect on primary production and distribution of prey) by calculating the temperature gradient for each CTD profile. Some temperature profiles were recorded at very shallow depths with some high temperature gradients in the upper layers, leading to a false identification of the thermocline depth. We also carried out a visual inspection of the temperature profiles of each tag to estimate the approximate thermocline depth, and removed the outliers located above this limit (a depth of up to 20 m). Euphotic depth (hereafter Zeu) was extracted to a grid of $0.25° \times 0.25°$ with a weekly resolution (used in SEAPODYM, provided by CLS, Toulouse) to investigate variations in the vertical accessibility of olive ridley prey (Lambert et al., 2014) and give a proxy of the water turbidity.

We performed a series of Linear Mixed Models (LMM) to relate the hunting time to water mass characteristics, using the R package *nlme* (Pinheiro et al., 2015) and following the steps described in Zuur et al. (2009). Collinear predictors were excluded (Spearman coefficients >0.7 and <−0.7), and the remaining covariates were included as fixed effects, i.e. the temperature at mean hunting depth (hereafter Hunting Temp), thermocline depth and euphotic depth. Salinity data were not incorporated in the LMM due to the low number of profiles recorded. All numeric variables were standardized, i.e. centered and scaled, allowing us to compare the magnitude of the effect for each predictor covariate (Péron et al., 2010). Turtle ID and the year of tag deployment were used as random effects. An autocorrelation term was also added to the models to account for temporal and spatial correlation between dives (Zuur et al., 2009). Similarly, a series of LMM was also fitted to assess the link between the mean hunting depth and oceanographic structures. All the combinations were tried without interactions, then the remaining covariates were incorporated and the models were compared using ANOVA before finally selecting the model with the lowest AIC (Burnham et al., 2011).

2.10. Statistical analysis

All statistical analyses were performed using R software version 3.2.1 (R Core Team, 2014). All samples submitted to statistical tests were first checked for normality and homogeneity of variances by means of the Shapiro–Wilk test. Parametric or nonparametric tests were then used, according to the results. Globally, Mann–Whitney *U* tests were used to compare the environmental variables among the two modes, i.e. transiting vs. foraging, using a significance level of $\alpha = 0.05$. Kruskal–Wallis tests were performed to account for differences between individuals. Values are means ± SD.

3. Results

3.1. Foraging behavior in the horizontal dimension

3.1.1. Trajectories and foraging grounds

The 20 olive ridley sea turtles fitted with either Argos-linked Fastloc GPS tags or CTD-SRDL measured 71.5 ± 2.5 cm CCL (range: 69–75 cm). The tag instruments transmitted on average 438 ± 330 locations, for a tracking duration ranging from 7 days (#130770) up to 229 days (#130765, Table 1). Two of the 10 turtles equipped during the inter-nesting season in 2014 did not transmit any data, namely individuals #136776 and #136777. In both years, the 18 remaining turtles headed northwestward and remained on the continental shelf off the shores of Suriname and French Guiana, mainly between 20 m and 100 m isobaths (Fig. 1). Only one turtle equipped in 2013 (#130771) reached the Venezuelan coast, traveling over 2776 km. The total distance traveled varied from 412 km (#130770) to 3651 km (#130765, mean: 1502 ± 689 km), whereas the forward linear path to reach foraging grounds was on average 366.8 ± 294.5 km, varying from 41.6 km to 1369 km (#130769 vs. #130771). The average observed speed was 0.45 ± 0.15 m s^{-1} (range: 0.25 ± 0.27–0.78 ± 0.61 m s^{-1}, #131355 vs. #130770, respectively). The real swimming speed corrected for oceanic currents ranged from 0.53 ± 0.32 to 1.10 ± 0.59 m s^{-1} (#131354 vs. #130769, respectively), with an average of 0.69 ± 0.17 m s^{-1}. Average elapsed time to reach the foraging grounds was 30 ± 17 d (range: 1–52 d, #130769 vs. #131355, respectively). The average ARS scale was 34.7 ± 25.6 km radius, ranging from 13 km to 100 km (#130765a and #130766 vs. #130765, respectively).

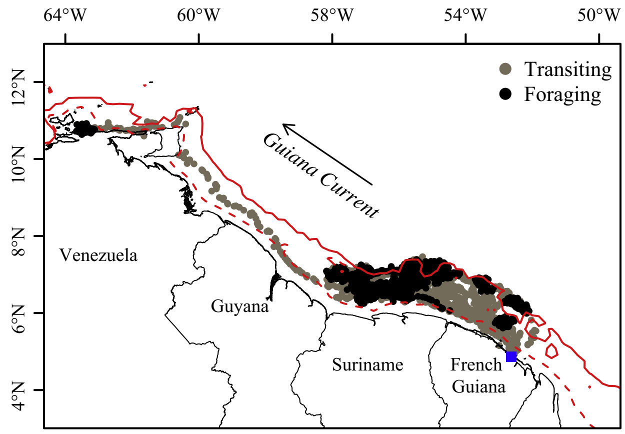

Fig. 1. Locations of the 18 olive ridley turtles equipped in 2013 ($n = 10$) and 2014 ($n = 8$) for the two behavioral modes, i.e. transiting (gray) and foraging (black). The blue square indicates the migration departure point, the dotted red line shows the 20 m isobaths and the solid red line indicates the 100 m isobaths.

3.1.2. Habitat use across the Guiana basin

On the Guiana basin scale, olive ridleys remained on the continental shelf during all the tracking duration, presumably avoiding the large eddies that are associated with higher SSH and maximum current velocities reaching up to 1.5 m s^{-1} (Fig. 2). The prevailing current were mainly northwestward, flowing at 0.53 ± 0.22 m s^{-1} at turtle's locations, and the individuals were associated with low SSH, on average 2.9 ± 3.8 cm. For both years of tag deployment, the micronekton biomass was aggregated at the edges of eddies (Fig. 3), supplying the continental shelf in micronekton biomass (mean: 1.7 ± 0.95 g WW m^{-2}). The foraging grounds of olive ridley sea turtles were therefore associated with higher micronekton biomass.

3.1.3. Habitat use at the tracking scale

During their post-nesting migration, olive ridleys remained in quite homogeneous habitats in terms of environmental conditions. Current velocity was slightly but significantly lower when turtles were foraging than when they were transiting (0.50 ± 0.20 vs. 0.58 ± 0.24 m s^{-1}, respectively, Mann–Whitney U test, $n = 7885$, $p < 0.001$, Fig. 2). The same pattern was observed for SST, with a very slight difference (28.25 ± 0.67 vs. 28.32 ± 0.65 °C, respectively, Mann–Whitney U test, $n = 7885$, $p < 0.001$). The turtles were associated with higher SSH at their foraging grounds (3.12 ± 3.86 vs. 2.48 ± 3.68 cm, respectively, Mann–Whitney U test, $n = 7885$, $p < 0.001$, Fig. 2) and deeper bathymetry than while transiting (81.9 ± 77.5 vs. 61.3 ± 63.0 m, respectively, Mann–Whitney U test, $n = 7885$, $p < 0.001$). Micronekton biomass during daytime and night were highly correlated, only micronekton during the day was retained for the analysis (Spearman correlation test: $R^2 = 0.99$, $p < 0.001$). The micronekton biomass during daytime was relatively high throughout migration for all individuals, and there was no significant difference in micronekton biomass during daytime between the two behavioral modes (1.76 ± 0.92 vs. 1.72 ± 0.97 g WW m^{-2}, respectively, Mann–Whitney U test, $n = 7885$, $p < 0.05$, Fig. 3).

3.2. Foraging behavior in the vertical dimension

3.2.1. Diving behavior from Argos-linked Fastloc GPS tags

The 8 Argos-linked Fastloc GPS tags deployed in 2013 provided 4055 records of maximum dive depth and 4583 records of dive

Table 1
Summary of the horizontal movements of the 18 olive ridleys tracked. Values are Mean + SD. PTT indicates individual turtle ID, Nloc the number of locations.

PTT	Start date	End date	Instrument	Nloc	Tracking duration (d)	Distance traveled (km)	Observed speed (m s^{-1})	Swimming speed (m s^{-1})
130764a	23/07/2013	29/09/2013	MK10	586	68	2384	0.58 ± 0.53	0.92 ± 0.52
130765a	20/08/2013	23/10/2013	MK10	457	64	2095	0.60 ± 0.56	1.10 ± 0.56
130766	07/08/2013	10/09/2013	MK10	193	34	1109	0.51 ± 0.50	0.72 ± 0.46
130767	22/07/2013	30/08/2013	MK10	174	39	1226	0.52 ± 0.49	0.72 ± 0.52
130768	04/08/2013	14/10/2013	MK10	262	71	2002	0.56 ± 0.56	0.66 ± 0.58
130769	21/07/2013	08/09/2013	MK10	288	49	1284	0.52 ± 0.58	1.10 ± 0.59
130770	05/08/2013	12/08/2013	MK10	36	7	412	0.78 ± 0.61	0.69 ± 0.54
130771	09/08/2013	05/10/2013	MK10	454	57	2776	0.76 ± 0.57	0.74 ± 0.59
131354	02/08/2013	20/11/2013	CTD-SRDL	1157	110	2174	0.31 ± 0.33	0.53 ± 0.32
131355	02/08/2013	28/12/2013	CTD-SRDL	1314	148	2237	0.25 ± 0.27	0.56 ± 0.30
130764	25/07/2014	15/10/2014	CTD-SRDL	235	82	1218	0.42 ± 0.48	0.60 ± 0.45
130765	02/08/2014	19/03/2015	CTD-SRDL	624	229	3651	0.31 ± 0.34	0.59 ± 0.32
136772	04/09/2014	29/10/2014	CTD-SRDL	223	55	795	0.30 ± 0.32	0.67 ± 0.34
136773	22/09/2014	12/12/2014	CTD-SRDL	285	81	1793	0.40 ± 0.43	0.55 ± 0.40
136774	28/08/2014	13/11/2014	CTD-SRDL	336	77	1632	0.37 ± 0.39	0.54 ± 0.34
136775	10/08/2014	10/10/2014	CTD-SRDL	268	61	1357	0.32 ± 0.37	0.59 ± 0.33
136778	03/08/2014	13/11/2014	CTD-SRDL	425	102	2075	0.35 ± 0.40	0.59 ± 0.38
136779	30/08/2014	28/12/2014	CTD-SRDL	568	120	2608	0.40 ± 0.43	0.59 ± 0.41
				438 ± 330	80.7 ± 49.6	1502 ± 689	0.45 ± 0.15	0.69 ± 0.17

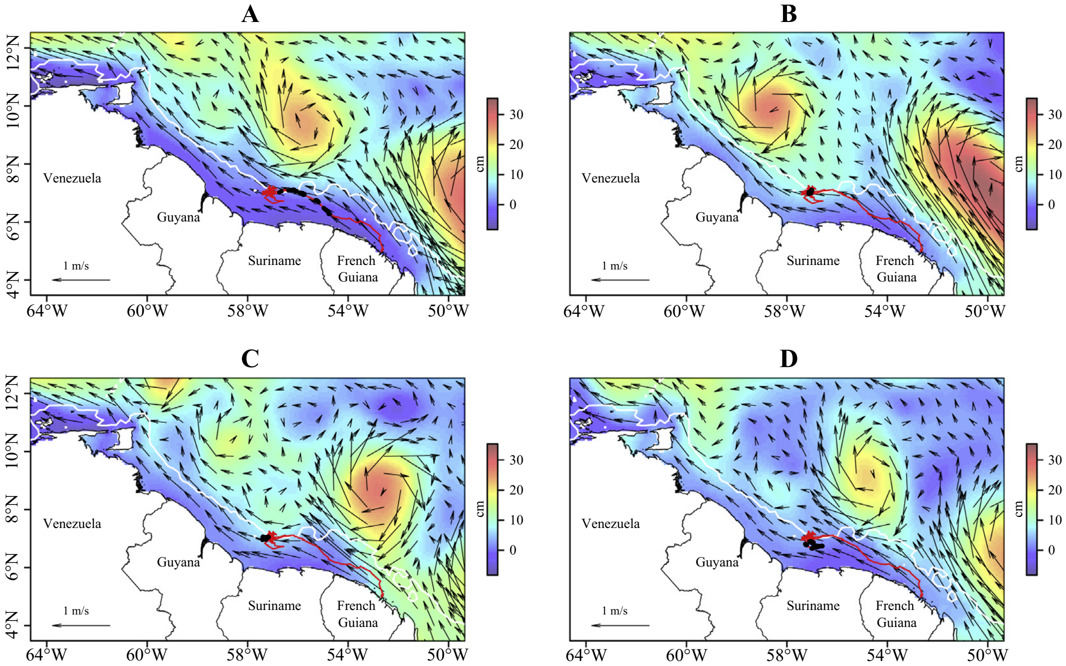

Fig. 2. Averaged direction and velocity of the currents over the whole study area for August 12–18/2013 (A), September 9–15/2013 (B), October 14–20/2013 (C) and November 11–17/2013 (D). The Sea Surface Height (SSH in cm, from the Mercator model) and the trajectory of the turtle #131354 (red solid line) were superimposed on oceanic currents (Mercator model). For a better visual representation, the spatial resolution of the current direction was set to 0.5° decimal. The black dots correspond to the locations of the turtle for the specific day and the white solid line the 100 m isobaths.

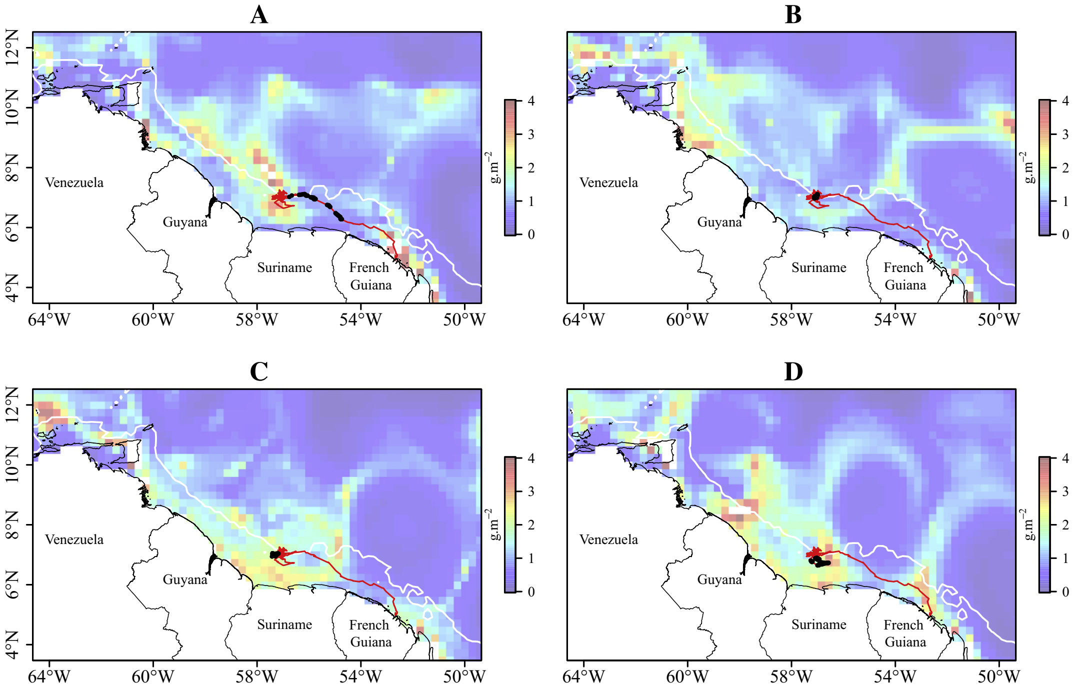

Fig. 3. Averaged micronekton biomass (g WW m^{-2}) predicted from SEAPODYM for August 12–18/2013 (A), September 9–15/2013 (B), October 14–20/2013 (C) and November 11–17/2013 (D) from SEAPODYM. The trajectory of the turtle #131354 (red solid line) was superimposed to micronekton. The black dots correspond to the locations of the turtle for the specific week and the white solid line the 100 m isobaths.

duration. Maximum dive depths varied from 0 to 200 m, with 45% of the dives performed in the upper 50 m (Fig. 4A). Maximum dive depths also differed significantly between individuals (Kruskal–Wallis rank sum test: $p < 0.001$, $n = 4055$).

Dive durations ranged from 30 s to 70 min, with 75% of the dives lasting between 30 and 70 min (Fig. 4B). Maximum dive durations differed significantly between individuals (Kruskal–Wallis rank sum test: $p < 0.001$, $n = 4583$).

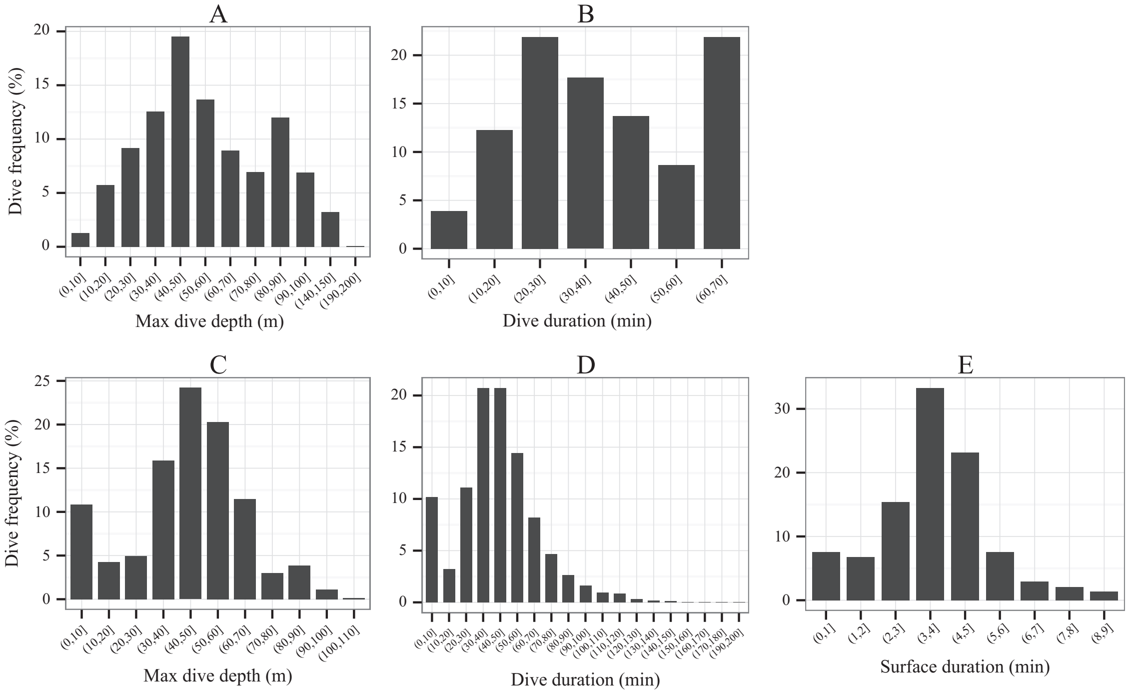

Fig. 4. Histograms of the diving variables recorded by the Argos-linked Fastloc GPS tags (A and B) and the CTD-SRDL tags (C, D and E). Maximum dive depth (A and C, m), dive duration (B and D, min), and post-dive surface interval (E, min) for all individuals.

3.2.2. Diving behavior from CTD-SRDL tags

The CTD-SRDL deployed in 2013 ($n = 2$) and 2014 ($n = 10$) provided reliable data for 2817 summarized dives profiles. Average maximum dive depth was 43.6 ± 20.6 m, ranging from 0 to 110 m (Fig. 4C). Maximum dive depths were significantly different between individuals (Kruskal–Wallis rank sum test, $p < 0.001$, $n = 2817$).

Dive durations varied from 30 s to 200 min (~3 h), lasted on average 45.9 ± 24.5 min and 40% of the dives lasted between 30 and 50 min (Fig. 4D). Dive durations differed significantly between individuals (Kruskal–Wallis rank sum test, $p < 0.001$, $n = 2817$).

Post-dive surface duration ranged from 0.06 s to 8.2 min, for an average duration of 3.6 ± 1.5 min. Sixty percent of the post-dive surface intervals lasted between 3 and 4 min, and differed significantly between individuals (Kruskal–Wallis rank sum test: $p < 0.001$, $n = 2817$) – see Fig. 4E.

Of the 2817 summarized dives retained for the analysis, 44% were benthic dives and 56% were pelagic dives with a difference between bathymetry and maximum dive depth $\geqslant 3$ m. Seventy percent of the turtles performed mainly pelagic dives (#131354, #131355, #130764, #130765, #136773, #136774 and #136779), and three individuals performed exclusively benthic dives (#136772, #136775 and #136778, Fig. 5).

The average Time of Allocation at Depth (TAD) was 0.8 ± 0.1, indicating mainly U-shaped dives (Table 2). Seventy-three percent of the dives recorded by the CTD-SRDL were associated with a TAD ranging between $0.75 \leqslant \text{TAD} < 0.1$.

3.2.3. In situ temperature and salinity data

The 1196 CTD profiles analyzed had recorded 21,775 temperature data and salinity data. Salinity ranged from 7.3 to 36.3 psu, and temperatures from 21.5 to 30.0 °C, and all turtles had used a broad range of oceanographic structures (Fig. 6A). The thermocline depth varied between 26.3 ± 2.3 m and 53.6 ± 9.4 m (#136778 vs. #136773, respectively, Fig. 6B), with an average depth of 43.4 ± 12.3 m (Table 2), and temperature profiles showed a horizontal stratification (Fig. 7A and B).

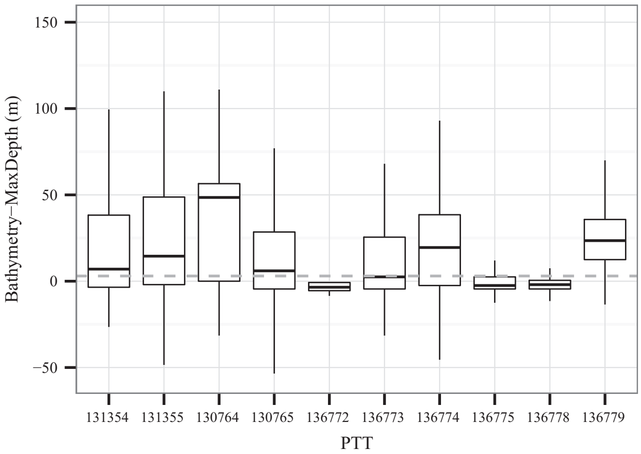

Fig. 5. Box plots of the depth difference between bathymetry and maximum dive depth of the 10 CTD-SRDL tags for each individual. The dotted line refers to the limit between benthic (depth difference $\leqslant 3$ m) and pelagic dives (depth difference >3 m).

3.2.4. Hunting time index

Among the 2817 dives recorded, 77% were discarded due to mismatches between the summarized dive and CTD profiles. Among the 647 remaining dives associated with a CTD profile (only temperature data were used due to the low number of salinity profiles), olive ridleys spent an average 36.4 ± 21.6 min hunting per dive, representing 77 ± 18.3% of the total dive duration (Table 2). Hunting time was negatively related to the euphotic depth and the temperature at mean hunting depth, the latter being the most significant covariate ($p < 0.05$ and $p < 0.001$, respectively, Table 3, Fig. 8A).

3.2.5. Mean hunting depth

The mean hunting depth ranged from 16.0 ± 14.8 to 50.1 ± 14.3 m (#131355 and #131354 respectively), with an

Table 2
Summary of the diving data associated with a temperature profile from CTD-SRDL tags. Values are Mean + SD and numbers in parentheses are the percentages. For each individual, Ndive refers to the number of dives that was associated with a temperature profile.

PTT	Instrument	*N* profile	TAD	Hunting time (min, %)	Hunting depth (m)	Hunting temp (°C)	Thermocline depth (m)
131354	CTD-SRDL	360	0.8 ± 0.1	36.7 ± 17.3 (82)	50.1 ± 14.3	26.0 ± 1.0	50.1 ± 7.3
131355	CTD-SRDL	79	0.8 ± 0.1	15.1 ± 15.0 (68)	16.0 ± 14.8	27.5 ± 0.5	28.8 ± 4.5
130764	CTD-SRDL	23	0.7 ± 0.1	30.4 ± 20.8 (74)	34.2 ± 14.7	26.4 ± 0.9	32.6 ± 4.9
130765	CTD-SRDL	75	0.7 ± 0.1	45.3 ± 36.8 (73)	27.1 ± 19.8	26.0 ± 1.2	36.6 ± 12.5
136772	CTD-SRDL	11	0.6 ± 0.2	27 ± 19.7 (62)	25.6 ± 15.6	26.2 ± 1.1	24.8 ± 4.7
136773	CTD-SRDL	51	0.8 ± 0.1	36.2 ± 25.5 (70)	48.9 ± 31.5	25.2 ± 1.8	53.6 ± 9.4
136774	CTD-SRDL	7	0.8 ± 0.1	39.1 ± 22.2 (68)	35.0 ± 15.7	26.4 ± 0.6	36.9 ± 1.8
136775	CTD-SRDL	16	0.7 ± 0.1	35.9 ± 27.5 (75)	30.3 ± 9.7	27.0 ± 0.6	31.2 ± 6.5
136778	CTD-SRDL	28	0.8 ± 0.1	34.1 ± 13.0 (77)	29.4 ± 6.9	26.7 ± 0.7	26.3 ± 2.3
136779	CTD-SRDL	62	0.7 ± 0.1	31.3 ± 19.2 (71)	35.0 ± 15.4	25.6 ± 1.1	34.2 ± 11.3
		71.2 ± 104.8	0.8 ± 0.1	36.4 ± 21.6 (77 ± 18.3)	43.5 ± 18.5	26.0 ± 1.1	43.4 ± 12.3

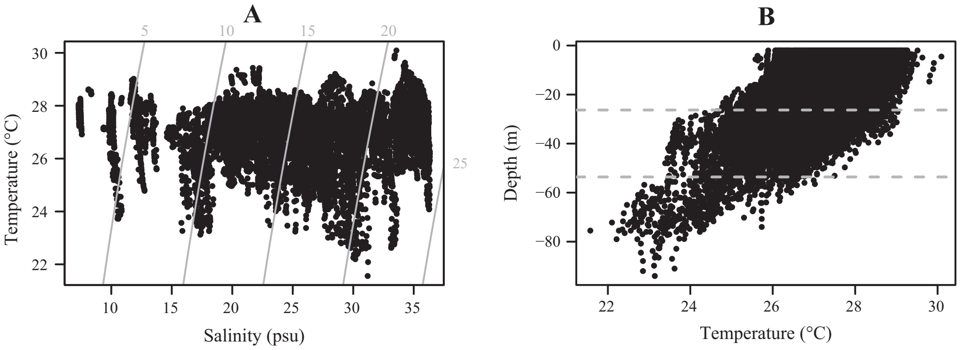

Fig. 6. T–S diagram (A) and temperature profile according to depth (B) for all individuals. The gray lines in A refer to the isopycnal lines and the dotted lines in B to the extrema of the thermocline depth.

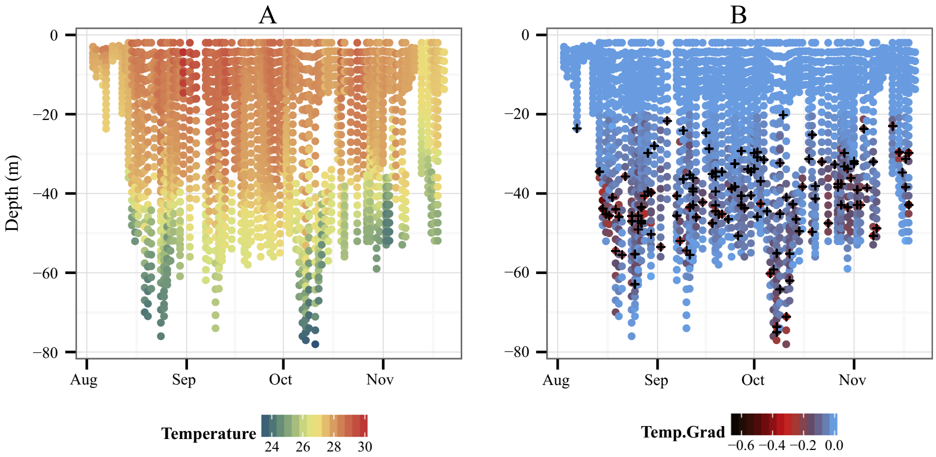

Fig. 7. CTD profiles of the *in situ* temperature (A, in °C) and temperature gradient (B, °C m^{-1}) for the individual #131354 throughout the tracking period. The black crosses in B refer to the mean hunting depths in each profile.

average of 43.5 ± 18.5 m and the average temperature at the mean hunting depth was 26.0 ± 1.1 °C (Table 2). Moreover, mean hunting depth was significantly related to the thermocline depth, the temperature at mean hunting depth and the euphotic depth (Table 4). Mean hunting depth increased with deeper thermocline (Fig. 8B) and euphotic depths ($p < 0.001$ and $p < 0.01$, respectively) and lower temperatures ($p < 0.001$, Table 4, Fig. 8C).

4. Discussion

This is the first study to use satellite telemetry-based movement tracking and diving behavior analysis to identify foraging activity in 18 adult female olive ridley sea turtles in both horizontal and vertical dimensions. We combined remote sensing data (SST, SSH and current velocity), micronekton predictions and *in situ* records (water temperature and salinity) to characterize the foraging activity of *Lepidochelys olivacea* at three different scales:

(1) Across the Guiana basin, taking into account the strong hydrodynamics driven by the retroflection of the North Brazil current.
(2) At the tracking scale, by comparing the habitat used during the transiting and the foraging modes identified.

Table 3
Summary of the selected model designed to relate the hunting time to the oceanographic variables of the water column. "Hunting temp" refers to the temperature at the mean hunting depth.

Response variable	Explanatory variable	Estimate	Std error	*Z* value	*p*-Value
Hunting time ~	Hunting temp	−481.6454	55.08959	−8.742948	<0.001
	Euphotic depth	−179.7802	73.66752	−2.440427	<0.05

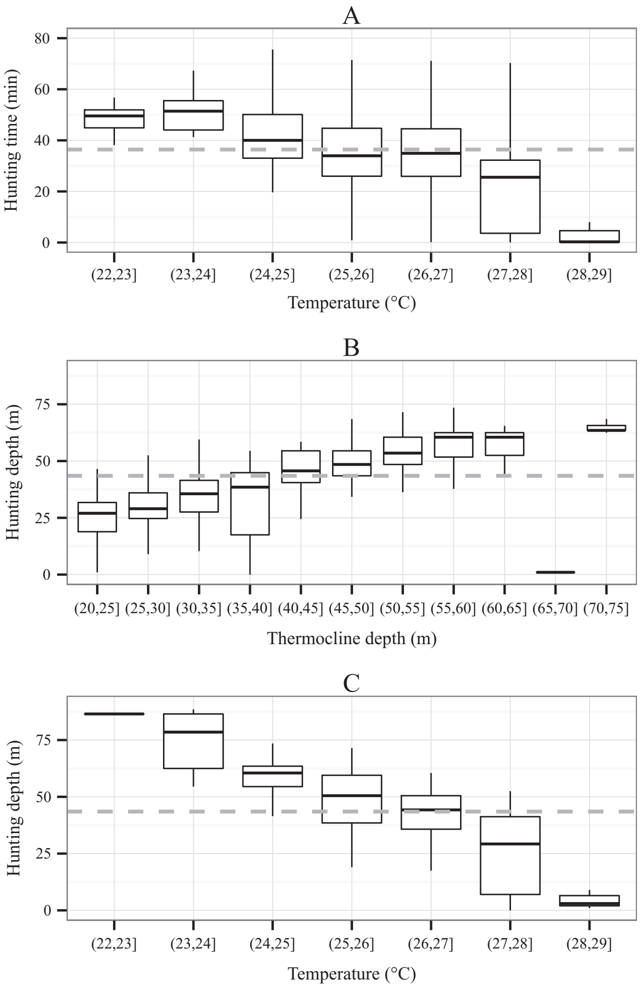

Fig. 8. Box plots of the most significant variables found with the models according to hunting time (A) and hunting depth (B and C). The dotted lines refer to the mean hunting time and mean hunting depth, respectively.

(3) And finally during dives, by relating the foraging activity occurring within dives to the properties of the water column.

4.1. Foraging activity across the Guiana basin

In this study, 18 olive ridleys were satellite tracked over seven months during their post-nesting migration from French Guiana. Although the tracking duration was relatively low for some individuals (mean: 80.7 d, range: 7–229 d), it was similar and even higher than the one of other studies on the same species (Whiting et al., 2007; Swimmer et al., 2009; Plot et al., 2015). Such low tag life could be firstly due to the very low levels of keratin of olive ridleys (Whiting et al., 2007), which prevented from cleaning properly the shell with scrapers to remove the entire epibiotic growth in the attachment area to make the epoxy stick firmly. Another cause of the relatively low tracking duration is probably the high levels of bycatch in the Guiana continental shelf (Fossette et al., 2014), especially regarding olive ridley sea turtles (Chevallier, unpublished data), clearly more subjected to this threat.

All individuals remained exclusively on the continental shelf, which contrasts with data from a previous study (Plot et al., 2015) that describes a higher behavioral plasticity in the migration dispersal, associated with the use of two other domains: continental slope and deep waters. However, all the turtles in our study performed a relatively short migration in terms of duration and distance to the foraging grounds (mean: 366.8 ± 294.5 km and 30 ± 17 d), which is in accordance with other studies on this species (Whiting et al., 2007; Rees et al., 2012; Plot et al., 2015), probably due to the short inter-breeding intervals of one to two years. Olive ridleys are also known to have different patterns in terms of spatial population structure, and the close proximity of the nesting and foraging areas highlighted in the present study is quite of unique.

The Guiana basin is known to be a highly dynamic zone under the influence of both the North Brazil Current and the South Equatorial Counter Current (Pauluhn and Chao, 1999). The merging of these two currents, called the North Brazil retroflection, generates anticyclonic eddies beyond the 500 m isobaths and thus drives the oceanic circulation of the continental shelf (Didden and Schott, 1993; Lumpkin and Garzoli, 2005). By remaining on the neritic domain, olive ridleys seem to target a stable and low turbulent area and therefore avoid being advected by the strong eddies and being swept away by the North Equatorial Counter Current. This occurred for one turtle tracked in 2006, which made a clockwise loop associated with oceanic currents and more specifically with one anticyclonic eddy (Plot et al., 2015). The movements of this single individual, probably due to navigational issues after being advected by the currents, support the idea that olive ridleys may deliberately avoid this highly turbulent area.

The French Guiana continental shelf is a productive zone (Muller-Karger et al., 1988; DeMaster et al., 1996) that is continuously supplied by the Amazon River plume. The warm-core anticyclonic eddies located off the French Guiana continental shelf are characterized by high SSH and SST at their core, and high micronekton biomass at their edge. This could explain why olive ridleys forage in this area during their post-nesting migration. The nutrient supply originating from the Amazon plume aggre-

Table 4
Summary of the selected model designed to relate mean Hunting depth to the oceanographic variables of the water column.

Response variable	Explanatory variable	Estimate	Std error	*Z* value	*p*-Value
Mean hunting depth ~	Thermocline depth	2.81159	0.514215	5.46774	<0.001
	Hunting temp	−12.75975	0.337562	−37.79973	<0.001
	Euphotic depth	1.76262	0.580940	3.03408	<0.01

gates at the edges of these eddies (Froidefond et al., 2002; Baklouti et al., 2007), making the continental shelf an area with a high concentration of organisms, from low- (phytoplankton) to high-trophic levels, including mid-trophic level (micronekton) through bottom-up processes, as shown in the Mozambique Channel (Sabarros et al., 2009). As olive ridley from the Sergipe (northeast Brazil) feeds mainly on crustaceans and small fish (Wildermann and Barrios-Garrido, 2012; Colman et al., 2014), this species is assumed to be a carnivorous consumer at the 3rd of even 4th trophic level. Olive ridleys might therefore target the edges of eddies to access food resources, probably composed of both pelagic and benthic organisms from the different micronekton functional groups, namely crustaceans, cephalopods, fishes and jellyfishes. This is consistent with the generalist feeding behavior of this carnivorous species, which shows a high plasticity (Bjorndal, 1985; McMahon et al., 2007). Stable isotope analyses are planned to be conducted to complete the present study, as skin samples have already been collected, and will be analyzed shortly to shed light on the organisms consumed by olive ridleys during their post-nesting migration along the Guiana coast.

Having described the habitat used by olive ridleys during their migration across the Guiana basin, we then sought to better characterize the habitat of *Lepidochelys olivacea* at their feeding grounds, relating the horizontal foraging activity to oceanographic and biological features provided by ocean circulation models.

4.2. Foraging activity at the tracking scale

Several foraging grounds were identified across the migration route using Residence Time analysis (Barraquand and Benhamou, 2008). The foraging activity occurred in areas of lower current velocity, which suggests that olive ridley sea turtles do indeed target areas of low turbulence rather than being passively advected by eddies. This behavior is supported by the tracking of seven olive ridleys equipped in the same location in 2006 (Plot et al., 2015), which six of them remained on the continental shelf, whereas only one was advected by eddies – see Plot et al., 2015 Supplementary materials. Additionally, turtles migrated in the same direction as the Guiana current, i.e. northwestward, suggesting that they used favorable currents to reach their foraging areas, probably to save energy. Similar patterns were observed in olive ridley turtles during their migration in the North Pacific Ocean, where they moved in the same direction as the North Equatorial Current (Polovina et al., 2006). However, the calculation of the real swimming speed corrected for current velocity indicated that all turtles swam presumably actively throughout the tracking duration. This suggests that they either target favorable habitats, i.e. weak currents, or possibly avoid unfavorable ones characterized by turbulent currents and eddies, as illustrated by the fact that rapidly leave the strong Guiana current at the beginning of the migration by heading westward, toward less turbulent waters.

To confirm the high swimming speed deduced from the ocean circulation model, it would have been necessary to assess the sensitivity of the Mercator model by using ‘control’ data from *in situ* surface drifters (Putman and He, 2013; Putman and Mansfield, 2015). However, due to the strong mismatch both in time and space between the satellite-derived outputs and the *in situ* data (http://www.aoml.noaa.gov/phod/dac/dacdata.php), such complementary analysis could not be performed in our study (Fossette et al., 2012a,b). Since we used the Mercator model which provides the highest spatial (0.08°) and temporal (daily) resolutions available to date (comparable to the Global Hybrid Coordinates Ocean Model), Mercator appears to be one of the most sophisticated and reliable tool to simulate ocean dynamics, limiting therefore the differences in velocity between drifter and model outputs ($\sim$3.5 cm s^{-1}) (Putman and He, 2013). As done recently by Putman and Mansfield (2015) on Kemp’s ridley and green turtles of the Mexico Gulf, a future study should be dedicated to the deployment of surface drifters alongside olive ridleys from the release site of Remire-Monjoly in French Guiana, to confirm the active swimming behavior of these females during their post-nesting migration.

In addition to the effect of prevailing currents on olive ridleys’ displacements, animal-borne instruments are known to induce additional drag, impacting therefore the animal behavior and energetics (Todd Jones et al., 2013). The tracked turtles measured 71.5 ± 2.5 cm (range: 69–75 cm), CCL close to those of Plot et al. (2015) taken on the same population in 2006 (mean: 68.1 ± 1.3 cm). Following Hays’ method (2001), CCL were converted into SCL (68.9 ± 2.2 cm) to get an estimate of the drag of each tag type. According to Todd Jones et al. (2013), and given the differences in tag size from both devices used in this study, the estimated drag would increase <5% for a MK10 tag and up to 20% for a CTD-SRDL fixed on a 68.9 cm SCL olive ridley. Furthermore, the swimming speed of the turtles fitted with a CTD-SRDL (0.5 ± 0.03 m s^{-1}) were significantly lower than those fitted with a MK10 tag (0.8 ± 0.18 m s^{-1}, Mann–Whitney U test: $p < 0.001$), this latter being nearly three times lighter than the CTD-SRDL devices (545 g vs. 192 g). Such difference shows the non-negligible effect of different animal-borne instruments on olive ridley’s behavior during their energetically costly migration phase. Biotelemetry-induced drag would therefore lead to an underestimation of the real swimming speed of this migratory species, reinforcing the need to deploy surface drifters alongside olive ridleys during their post-nesting migration from French Guiana.

The stable areas targeted are globally associated with high primary productivity, i.e. enriched waters discharged by the Amazon plume, but the foraging activity is not necessarily associated with a specific patch of higher micronekton biomass for all turtles, as the whole continental shelf is characterized by a high productivity. The relatively homogeneous habitats crossed by olive ridleys during their migration could also explain part of this mismatch: differences in terms of environmental values are not always significant when comparing the transiting vs. foraging mode. However, the micronekton biomass remains relatively high in both modes, compared to that found in the core of eddies. Rather than classically considering chlorophyll *a* concentrations or primary production as biological variables (Polovina et al., 2006; Kobayashi et al., 2008; Dalleau et al., 2014), this study is the first to use SEAPODYM outputs to relate olive ridley foraging activity to the distribution of their prey. However, it is important to note that our micronekton data come from model predictions, which are not devoid of uncertainty. In some cases, there can be some differences between the model outputs and *in situ* measurements (Mulet et al., 2012), especially in coastal regions under the influence of a large river such as the Amazon. Given the weekly averaged data of SEAPODYM, the occasional mismatch between olive ridley foraging locations and high micronekton biomass could also be due to the lag between prey distribution and sea turtle movements. However, SEAPODYM outputs are arguably robust enough to provide accurate estimations on the regional scale (Lambert et al., 2014) and provide relative biomass values, which in our case is a sufficient estimation of olive ridley preys. Furthermore, ongoing experiments to validate and assimilate acoustic data are currently being validated to make this model more robust and provide a higher resolution.

As a physiographic variable, deep bathymetry was highly associated with foraging activity as olive ridleys favored deeper waters of between 40 and 200 m at their foraging grounds, probably to avoid the higher water turbidity close to the shore, caused by the nutrient supply from the Amazon and other rivers (Anthony et al., 2010). By targeting clearer waters, turtles could potentially have more visibility to catch prey, while avoiding predators. This bathymetry is probably also related to diving behavior, characterized by both pelagic and benthic dives.

In accordance with previous studies (McMahon et al., 2007; Hamel et al., 2008; Plot et al., 2015), the dives were mainly U-shaped, i.e. with the core of activity centered at the bottom of the dive (Fedak et al., 2001). Fifty-six percent of the dives were pelagic, and 44% were benthic. Our data confirm that olive ridleys mainly rely on pelagic preys in the Atlantic, and accord with data obtained in the Pacific (Polovina et al., 2006). As previously observed in olive ridleys migrating from French Guiana (Plot et al., 2015), our data also highlight strong differences in the diving behavior among individuals. This could enable this species to use the numerous foraging grounds we identified on the continental shelf, sometimes several hundred kilometers apart. Alternatively, this plasticity could be due the heterogeneity of the local conditions encountered, which probably fluctuate drastically among individuals, and force the turtles to behave differently.

This study enabled us to relate the horizontal foraging activity of olive ridleys to surface environmental variables throughout migration. This species performed a short migration, crossing relatively homogeneous habitats in terms of surface features, namely current velocity, SST, SSH and micronekton biomass. The analysis of the foraging activity in the vertical dimension is complementary and essential, being based on *in situ* data of the water column, and also proved very useful to understand the foraging behavior of olive ridley turtles.

4.3. Foraging activity at the dive scale

By remaining exclusively on the continental shelf, all turtles swam in the tropical surface waters (Stramma and Schott, 1999), but crossed highly stratified waters, especially in terms of salinity. A large number of rivers along the Guianan coast flow into the Equatorial Atlantic, affecting the salinity of the waters (Froidefond et al., 2002) and consequently the primary production and turbidity of the continental shelf. Off the shores of French Guiana, the neritic domain is composed of three water classes that are best distinguished by their reflectance, i.e. beige waters close to the coastline, green waters above the 20 m isobaths and low salinity dark brown waters originating from the Amazon plume (Froidefond et al., 2002). A thick layer of 5–7 m extending up to 80 km offshore is characterized by low salinity, i.e. 17–24 psu, which is consistent with the salinity data recorded by the tags. As turtles focus their foraging activity at depths where salinity variability is thought to be rather limited, it is unlikely that the salinity distribution would act as a major constraint on turtle behavior. Unlike the green waters close to the shore with low chlorophyll *a* concentrations due to high suspended matter, the dark brown waters, i.e. an area off the 20 m isobaths and inhabited by olive ridleys, are characterized by high concentrations of dissolved organic matter and chlorophyll *a*. Our results support the idea that olive ridleys continuously forage during dives in areas of high productivity, with hunting time accounting for an average 77% of the dive duration.

The *in situ* temperatures recorded varied from 21.5 to 30.0 °C, and show a broader thermal range than those seen in previous studies. This is partly because the temperatures recorded in other studies did not have access to *in situ* temperatures and used SST instead (Polovina et al., 2006; McMahon et al., 2007; Swimmer et al., 2009). Comparison of the SST ranges showed that our data (range: 26.1–29.9 °C) are similar to the narrow thermal range of 5 °C observed in olive ridleys studied in the Pacific or those from the Atlantic (Polovina et al., 2006; McMahon et al., 2007; Plot et al., 2015), but with however warmer temperatures. These differences in thermal range may be explained by the warm water supply coming from the Amazon River (Nikiema et al., 2007). As *in situ* temperature plays an important role in the vertical foraging activity of olive ridley sea turtles, hunting time increased with the drop in water temperature. Sea turtles are ectothermic organisms, and may regulate their body temperature by reducing their metabolism thanks to cooler layers within the water column (Caut et al., 2008). The cooler temperatures may also affect the distribution of olive ridley prey.

Thermal stratification in the water column resulted in a thermocline depth ranging from 26.3 to 53.6 m, which is highly correlated to the mean hunting depth. The deeper the thermocline, the hunting depth increased, indicating that olive ridleys preferentially target areas within and below the thermocline depth. Similar behaviors have been reported in seabirds and marine mammals (Ballance et al., 2001; Charrassin and Bost, 2001). The thermocline plays a crucial role in the vertical distribution of pelagic preys (Hakoyama et al., 1994) and ultimately affects the foraging success of marine megafauna species (Benoit-Bird et al., 2013). Also, the sharp change in water temperature induces changes in water density and therefore concentrates organic matter, resulting in a rich source of food for zooplankton. Through bottom-up processes, the micronekton that aggregates at these depths is followed by carnivorous species such as olive ridley sea turtles (Field et al., 2001). By targeting in and below the thermocline depth, *Lepidochelys olivacea* migrating from French Guiana adopt the same behavior as loggerhead turtles from the Pacific, diving at relatively shallow thermocline depths (Polovina et al., 2006). Furthermore, the analysis of stomachal contents performed on olive ridleys caught in Hawaii indicated that this species feeds on pelagic organisms distributed in the subsurface layers of the water column, i.e. pyrosomes (*Pyrosoma atlantica*) and salps (Salpidae) (unpublished data, Honolulu Laboratory, NMFS). The layers of prey aggregation for olive ridleys may therefore be found at and beyond the thermocline depth.

Euphotic depth is the final major oceanographic variable found to play a role on olive ridley foraging activity during dives. Photosynthesis can no longer be supported below this depth due to light deficit (Kirk, 2011), and we observed a longer hunting time in shallower euphotic depths. The prediction of cetacean densities based on SEAPODYM outputs have shown that waters with shallow euphotic depths were associated with higher micronekton biomass in the Southwest Indian Ocean, and conversely, waters with deep euphotic depths in French Polynesia had low micronekton biomass (Lambert et al., 2014). Based on this assumption, the olive ridley may target shallow euphotic depths to access higher concentrations of prey. In contrast, mean hunting depth increased with euphotic depth, suggesting that turtles foraged exclusively within the euphotic zone, where light penetration ensures higher primary production than in deeper layers.

In this study, olive ridley's foraging success was for the first time calculated using the hunting time index as defined in Heerah et al. (2015). Hunting time took up an average 77% of the dive duration, indicating that turtles foraged quasi-continuously during dives, even while transiting (identified via Residence Time Analysis). This result suggests an opportunistic behavior of *Lepidochelys olivacea*, which is consistent with the generalist diet of this species (Bjorndal, 1985; McMahon et al., 2007). However, the lack of high resolution data makes it impossible to validate the vertical speed threshold used to differentiate between transit and hunting modes within-dives. As this approach was adapted from other species, it would be useful to validate this threshold by retrieving the tags during the next inter-nesting season, and thereby also confirm the foraging events detected within each dive. To ensure the correct identification of the different activities of olive ridleys within dives, it would also be interesting to use acceleration data loggers in a further study, as already performed in leatherback turtles (Fossette et al., 2010a,b). This is of particular interest to glean more information about the diving behavior of olive ridley, which remains little documented to date.

5. Conclusion

The present study describes the foraging behavior of the olive ridley sea turtle in relation to its environment, during post-nesting migration from French Guiana, and significantly reinforces the previous study on the species in this region (Plot et al., 2015). The foraging activity of *Lepidochelys olivacea* was assessed in both horizontal and vertical dimensions through the use of movement tracking data and diving behavior analysis that was carried out via an innovative proxy of the vertical foraging activity, namely the hunting time index. The combination of complementary sources of environmental data and techniques provides a description of the habitat used on three different scales: across the Guiana basin, during the tracking period and within dives. Across the Guiana basin and on the tracking scale, the use of remote sensing data and micronekton predictions highlights the influence of the strong currents that generate anticyclonic eddies and therefore spread the nutrients originating from the Amazon River. This circulation therefore benefits olive ridleys during migration to their feeding grounds. At the finest scale, i.e. the dive level, the use of *in situ* temperature sheds light on the crucial role of the thermocline in the foraging behavior of olive ridleys within dives, suggesting an influence of the temperature in both the regulation of turtle metabolism and prey distribution within the water column. Further investigation into the diet of this species and its foraging activity in the Equatorial Atlantic is required to better understand the feeding ecology of the olive ridley and estimate its prey capture attempts.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.pocean.2016.01.006.

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ANNEXE G

The Gulf Stream frontal system : A key oceanographic feature in the habitat selection of the leatherback turtle ?

P. Chambault, F. Roquet, S. Benhamou, A. Baudena, B. de Thoisy, E. Pauthenet, R. Crasson, M. Brucker, M. Bonola, V. Dos Reis, Y. Le Maho, D. Chevallier. 2017. The Gulf Stream frontal system : A key oceanographic feature in the habitat selection of the leatherback turtle ? Deep-Sea Research Part I. 123. 35-47. 10.1016/j.dsr.2017.03.003.

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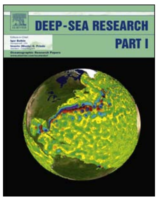

The Gulf Stream frontal system: A key oceanographic feature in the habitat selection of the leatherback turtle?

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ABSTRACT

Although some associations between the leatherback turtle *Dermochelys coriacea* and the Gulf Stream current have been previously suggested, no study has to date demonstrated strong affinities between leatherback movements and this particular frontal system using thorough oceanographic data in both the horizontal and vertical dimensions. The importance of the Gulf Stream frontal system in the selection of high residence time (HRT) areas by the North Atlantic leatherback turtle is assessed here for the first time using state-of-the-art ocean reanalysis products. Ten adult females from the Eastern French Guianese rookery were satellite tracked during post-nesting migration to relate (1) their horizontal movements to physical gradients (Sea Surface Temperature (SST), Sea Surface Height (SSH) and filaments) and biological variables (micronekton and chlorophyll *a*), and (2) their diving behaviour to vertical structures within the water column (mixed layer, thermocline, halocline and nutricline). All the turtles migrated northward towards the Gulf Stream north wall. Although their HRT areas were geographically remote (spread between 80–30 °W and 28–45 °N), all the turtles targeted similar habitats in terms of physical structures, i.e. strong gradients of SST, SSH and a deep mixed layer. This close association with the Gulf Stream frontal system highlights the first substantial synchronization ever observed in this species, as the HRTs were observed in close match with the autumn phytoplankton bloom. Turtles remained within the enriched mixed layer at depths of 38.5 ± 7.9 m when diving in HRT areas, likely to have an easier access to their prey and maximize therefore the energy gain. These depths were shallow in comparison to those attained within the thermocline (82.4 ± 5.6 m) while crossing the nutrient-poor subtropical gyre, probably to reach cooler temperatures and save energy during the transit. In a context of climate change, anticipating the evolution of such frontal structure under the influence of global warming is crucial to ensure the conservation of this vulnerable species.

1. Introduction

Oceanic fronts are transition areas between water masses of contrasting properties (Belkin et al., 2002; Scales et al., 2014). These sharp boundaries are generally characterized by physical and biological discontinuities in terms of temperature, salinity and nutrient gradients (Le Fèvre, 1986; Reul et al., 2014; Scales et al., 2014; Greer et al., 2015), and occur across a variety of spatial and temporal scales, from sub-mesoscale (1–10s km) to ocean basin scales (1000s km). Oceanic fronts can be generated by various physical processes, ranging from the presence of an estuary or a shelfbreak, the occurrence of locally enhanced tidal mixing, wind-induced upwelling or convergence patterns, the presence of sea ice or the western intensification of gyre circulations (Belkin et al., 2009).

The physical processes (upwelling, mixing, stirring) generating oceanic fronts lead to increased primary and secondary productivity (Olson and Backus, 1985; Olson et al., 1994), enhancing in most cases the activity at higher trophic levels via bottom-up processes (Le Fèvre, 1986; Largier, 1993; Acha et al., 2004). Frontal systems are therefore commonly associated with a diverse range of marine vertebrates such

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as seabirds (Haney and McGillivary, 1985, van Franeker et al., 2002; Cotté et al., 2007; De Monte et al., 2012; Scheffer et al., 2012; Thorne and Read, 2013; Whitehead et al., 2016), pinnipeds (Bradshaw et al., 2004; Bailleul et al., 2010; Nordstrom et al., 2013), cetaceans (Moore et al., 2002; Etnoyer et al., 2006; Doniol Valcroze et al., 2007; Druon et al., 2012; Murase et al., 2014) and sea turtles (Eckert et al., 2006b; Fossette et al., 2010a; Witherington, 2002; Polovina et al., 2004; Polovina and Howell, 2005).

The largest frontal system in the North Atlantic Ocean is associated with the Gulf Stream, one of the World hydrodynamic oceanic currents (Schmitz and McCartney, 1993; Lozier et al., 1995; Ducet et al., 2000). Forming the western boundary current system of the North Atlantic Ocean subtropical gyre, this fast current originates in the Gulf of Mexico and intensifies along the south-east coast of the United States before leaving the coastline to cross the Atlantic Ocean at about 40 °N. A strong thermal boundary occurs at the intersection of the warm, salty Gulf Stream waters and the cold and less salty waters of the Labrador Current (Fuglister, 1963). Like in other frontal systems, some associations have been observed between the Gulf Stream and marine megafauna (Olson et al., 1994) such as seabirds (Haney and McGillivary, 1985; Thorne and Read, 2013), fish (Block et al., 2001, 2005; Wilson et al., 2004; Skomal et al., 2009; Potter et al., 2011) and sea turtles (loggerhead: Witherington, 2002; leatherback: Eckert et al., 2006b; Fossette et al., 2010a; Lutcavage, 1996; Dodge et al., 2014).

While the leatherback turtle (*Dermochelys coriacea*) has often been tracked in the Atlantic Ocean (Bailey et al., 2012b; Eckert et al., 2006b; Fossette et al., 2010b, 2010a; James et al., 2005a, 2005b; Ferraroli et al., 2004; Hays et al., 2004; McMahon and Hays, 2006; López-Mendilaharsu et al., 2009; Dodge et al., 2014), only a few studies have suggested that this species may associate with the Gulf Stream frontal system (Eckert et al., 2006b; Fossette et al., 2010a; Lutcavage, 1996). More recently, Dodge et al. (2014) have shown a relationship between leatherback movements and strong Sea Surface Temperature (SST) gradients, highlighting some affinities for the Gulf Stream front, but only for a limited number of individuals (n=2), and not in the vertical dimension. Given that the Gulf Stream frontal system is marked by strong SST gradients and pronounced vertical mixing, aggregating therefore low trophic level organisms such as jellyfish (Sims and Quayle, 1998; Greer et al., 2013; Powell and Ohman, 2015), it would be logical to expect North Atlantic leatherback turtles to interact with the Gulf Stream frontal system during their post-nesting migration across the North Atlantic. We propose in this study to examine more systematically the potential affinities of leatherback turtles with this frontal system based on detailed 3D oceanographic data, investigating both the geographical patterns and the vertical dive behaviour in relation to physical and biological ocean conditions.

This study assesses the role of the Gulf Stream frontal system in the selection of preferentially used areas by the leatherback turtle via the satellite tracking of 10 adult females, equipped between 2014 and 2015 from the Eastern French Guianese rookery. This is one of the two major rookeries for the leatherback turtle on the west coast of the equatorial Atlantic (Fossette et al., 2008), showing a different genetic structuration (Molfetti et al., 2013). Note that several female leatherback turtles from the Western French Guianese population have been tracked in the past (Fossette et al., 2010b, 2010a), but it is the first time tracks from the Eastern rookery are documented. After identifying high residence areas (a proxy of foraging grounds), we used a series of biological and physical variables provided by 3D ocean reanalysis products to relate (1) the horizontal movements of the leatherback turtles to physical properties (SST and Sea Surface Height (SSH) gradients and filaments) and biological variables (micronekton and chlorophyll a), and (2) their diving behaviour to vertical structures within the water column (mixed layer, thermocline, halocline and nutricline).

2. Materials and methods

2.1. Ethics statements

This study met the legal requirements of the country in which the work was carried out (France), and followed all institutional guidelines. The protocol was approved by the “Conseil National de la Protection de la Nature” (CNPN, http://www.conservation-nature.fr/acteurs2.php?id=11), which is under the authority of the French Ministry for ecology, sustainable development and energy (permit Number: 2015133-0022), and acts as the ethics committee for French Guiana. The fieldwork was carried out in strict accordance with the recommendations of the Police Prefecture of Cayenne (French Guiana, France), to minimize any disturbance of the animals.

2.2. Study area and tag deployment

During the 2014 and 2015 nesting seasons, 11 adult female leatherback turtles were equipped with satellite tags on the beaches of Rémire-Montjoly (4.53°N–52.16°W, Cayenne, French Guiana). One Argos Fastloc GPS tag (SPLASH10-F-296A, Wildlife Computers Redmond, WA, USA) was deployed in August 2014 and 10 Satellite Relay Data Loggers (SRDL, Sea Mammal Research Unit, University of St. Andrews, Scotland) were deployed in June 2015. These tags were attached during night-time egg laying, i.e. at the only moment when individuals are static while ashore. Harnesses were not used to attach the satellite tags in order to minimize hydrodynamic drag. Prior to attachment, the tags were moulded into a resin mount to match the shape of the central dorsal ridge, and two holes were drilled into the resin mount for the stainless steel cable. The attachment area was disinfected with Betadine then locally anesthetised with Lidocaïne © spray. Two <0.5 cm diameter holes were drilled into the central dorsal ridge. The tags were then fixed by threading a stainless steel cable through the holes in the dorsal ridge and the resin tag mount. Stainless steel crimps were used to secure the cable and were covered with an epoxy resin to ensure solidity, preventing the tag from being released before the return of the turtles to the nesting site (French Guiana) in 2–4 years.

2.3. Data collected from the tags

Both tag types recorded horizontal (Argos and/or GPS locations) and vertical movements (diving behaviour) of the turtles, but at different resolutions.

2.3.1. Argos Fastloc GPS tag

The single Argos Fastloc GPS tag deployed in 2014 recorded both Argos and GPS locations (every 4-h), as well as depth data describing specific diving parameters, namely maximum dive depths, dive durations, and *in situ* temperature data, binned as 4-h period histograms. The wet/dry sensor of the tag was used to identify the beginning and end of each dive. The sensor entered haul-out state after 20 consecutive dry minutes, and exited haul-out state if it remained wet for 30 s or more. Maximum depths were collected in different bins, every 10 m from 10 to 100 m, then every 50 m from 100 to 250 m with a depth sensor accuracy of 1% of reading. Similarly, maximum dive durations were stored from 30 s to 1 min, then every minute from 1 to 5 min, every five minutes from 5 to 20 min, and *in situ* temperatures from 20 to 32 °C were recorded during dives with a resolution of 1 °C, with a temperature sensor accuracy of 0.1 °C. This tag also supplied Time At Depth (TAD), defined as the proportion of time (in %) spent at each depth.

2.3.2. SRDL tags

One of the 10 SRDL tags deployed in 2015 did not transmit any data, and was therefore excluded from the analysis. The other nine SRDL tags provided Argos-based location data, as well as data about diving behaviour including dive depth (with a depth sensor resolution of 0.5 m), dive duration and duration of post-dive surface intervals. The wet/dry sensor of the tag was used to identify the beginning and end of each dive. Dives started when the sensor was wet and below 1.5 m for 20 s, and ended when dry or above 1.5 m. The SRDL tags were programmed to send summarized dive profiles using the compression algorithm described by Fedak et al. (2001), with 4 depth records for each dive (instead of 1 maximum depth per dive for the Argos Fastloc GPS tag).

2.4. Data pre-filtering

As all tags were deployed during the nesting season, they recorded movements and diving behaviour for both the nesting and migration phases. Following the procedure described in Chambault et al. (2015), we excluded the nesting phase to focus on the migration phase alone. A Kalman filtering algorithm (Silva et al., 2014; Lopez et al., 2014) provided by Collecte Location Satellites (CLS Toulouse, France) was applied to estimate Argos locations. Basically, the algorithm uses a correlated random walk model to predict the next location and its associated error based on the previous positions and estimated error. To each Argos location was assigned a Location Class (LC): 3, 2, 1, 0, A, B or Z. Approximately 17% of the locations of our study were associated with an estimated error (from > 250 m to > 1500 m, LC 3: 2.1%, 2: 4.3%, 1: 5.6% and 0: 5.7%), 83% had no accuracy estimation (LC A: 20.5% and B: 61.7%), and 1% were invalid (LC Z). The GPS locations (provided by the single tag deployed in 2014) were associated with an accuracy < 100 m (0.1% recorded). We used the General Bathymetric Chart of the Oceans (GEBCO) database (http://www.gebco.net/, resolution 30 arc-second, ~1 km grid) to discard any locations on land. As described in Fossette et al. (2010a), we also discarded the Argos locations associated with a speed of over 10 km h^{-1} (9% in 2014 and 10% in 2015, Fossette et al., 2010b), as well as “type Z” (i.e. invalid Argos-based) locations.

2.5. Current correction of tracks

Tracks were first re-sampled according to the mean daily locations frequency obtained for both tag types: every 2 h (Argos-GPS) or 8 h (SRDL). We then corrected the ground-related (satellite-recorded) tracks for oceanic currents to estimate the movements of leatherbacks according to the water masses they cross, providing a more accurate picture of actual movement behaviour (Girard et al., 2006; Gaspar et al., 2006). Surface current velocity fields can be computed as the vectorial sum of geostrophic and Ekman components (Sudre et al., 2013). The geostrophic component results from the balance between the horizontal pressure gradient force and the Coriolis force. It was computed from the Ssalto/Duacs maps of absolute dynamic topography data available daily on a 1/4 ° grid (www.aviso.altimetry.fr/en/data/products/sea-surface-height-products/global/madt-h-uv.html) based on an updated assessment of the sum of sea level anomalies and mean dynamic topography, both being referenced over a twenty-year period in the Duacs 2014 version (V15.0). The Ekman component results from the balance between friction by wind and the Coriolis force. It was estimated from wind stress data provided daily on a 1/4° grid by CERSAT IFREMER (Ascat daily gridded mean wind field: http://cersat.ifremer.fr/data/products/catalogue). Both geostrophic and Ekman components were computed using a recent model (GEKCO product) developed by Joël Sudre and underwent a bi-linear spatial interpolation and a linear temporal interpolation to estimate their "meridional" (i.e. E-W) U and "zonal" (i.e S-N) V components at every turtle's location (velocity field data and a user-friendly program to interpolate local values at any location and time are freely available at www.legos.obs-mip.fr/sudre). It is worth noting however that the Ekman component becomes negligible under the mixed layer (e.g. within the thermocline, Marshall and Plumb, 2007). We therefore estimated the proportion P of time spent above the thermocline for each dive of each turtle, and computed the real current velocity as:

$$U_{actual} = U_{geostrophic} + P.\ U_{Ekman} \quad \text{and} \quad V_{actual} = V_{geostrophic} + P.\ V_{Ekman}$$

The time spent above the thermocline could not be calculated for the Argos-GPS tag deployed in 2014 due to the coarser resolution of the diving data. For this turtle, P was estimated as a function of the location based on the diving data provided by the 9 other tags. Finally, the water mass-related (i.e. "motor") step lengths for each turtle were computed as:

$$\Delta X_{motor} = \Delta X_{track} – \Delta t.\ U_{actual} \quad \text{and} \quad \Delta Y_{motor} = \Delta Y_{track} – \Delta t.\ V_{actual}$$

where ΔX_{track} and ΔY_{track} are ground-related step lengths based on coordinates of the satellite-recorded locations (converted from longitude and latitude to an orthonormal metric system X and Y), and Δt is the time of movement between a given location and the next (see Girard et al., 2006 for details).

2.6. Residence time analysis

We inferred high residence time (HRT) phases (and therefore HRT areas) by applying Residence Time (RT) analysis (Barraquand and Benhamou, 2008; Benhamou and Riotte-Lambert, 2012) to the current-corrected movements. The RT for a given location indicates the time spent within a circle centred on this location with a given radius R. It is therefore computed as the difference between forward and backward first passage times at distance R from the centre, plus possible additional backward and/or forward times spent within the circle provided that the animal does not leave the circle for more than a given time (set to 8 h in the present study), before returning within the circle. The circle runs along the path in this approach, providing a more contrasted and less noisy time series (with respect to simpler analyses based on first passage times). As advised in Barraquand and Benhamou (2008), we computed RT time series with a radius r ranging between 10 and 100 km to explore different scales. The low residence time (hereafter LRT) and HRT areas for the migration of each turtle were then inferred by segmenting RT time series using Lavielle (2005) segmentation method.

2.7. Environmental data

2.7.1. Horizontal variables

We extracted a series of environmental variables from both remote sensed data and model simulations to characterize the habitat of leatherback turtles at their HRT areas. The variables selected were those most likely to influence the distribution of jellyfish (Graham et al., 2001). We extracted the surface sea water chlorophyll *a* concentration at each turtle location from the *Global ocean biochemical analysis and forecast* product (BIO 001–014) at a 0.5 ° spatial resolution (from U.E Copernicus Marine Service Information: http://marine.copernicus.eu/services-portfolio/access-to-products/).

As the *Spatial Ecosystem And Population Dynamics Model* (SEAPODYM) predicts the spatio-temporal distribution of micronekton (Lehodey et al., 2008, CLS Toulouse), the smallest pelagic organisms capable of swimming against sea currents (individuals measuring from 2 to 25 cm), it was used to estimate the distribution of leatherback prey. It includes the diet of leatherback turtles and encompasses different micronekton groups, including jellyfish (Brodeur et al., 2005). Micronekton is modelled using current and temperature data provided by the *GLobal Ocean ReanalYsis and Simulations* product (GLORYS-2v1), and net primary production and euphotic depth derived from ocean colour satellite data (http://www.science.oregonstate.edu/ocean.productivity/) using the *Vertically Generalised Production Model* (VGPM). Due to the lack of micronekton predictions in nearshore mesopelagic and bathypelagic layers, we estimated only the epipelagic layer using this model. To investigate variations in the vertical accessibility of leatherback prey, we also extracted the euphotic depth weekly on a grid of 0.25 °×0.25 °.

Table 1
Summary of the horizontal post-nesting movements of the 10 leatherback turtles tracked. Speed values are Mean ± SD. PTT refers to the turtle's ID, Nloc to the number of locations, HRT to high residence time.

Ptt	Tag type	Start date	End date	Nloc	Tracking duration (d)	Distance (km)	Daily speed (km d^{-1})	Duration to HRT areas (d)
131347	SPLASH10-F	28/08/2014	25/01/2015	1798	150	6794	44.9 ± 29.0	92
149680	SRDL	30/07/2015	06/11/2015	297	99	4957	49.6 ± 25.9	65
149681	SRDL	06/07/2015	12/12/2015	479	159	7122	44.5 ± 21.4	92
149682	SRDL	18/07/2015	03/02/2016	579	200	8080	40.8 ± 34.0	111
149683	SRDL	16/07/2015	12/11/2015	357	119	5093	42.4 ± 19.6	79
149684	SRDL	08/07/2015	07/12/2015	454	152	7093	46.3 ± 22.8	115
149685	SRDL	14/07/2015	21/02/2016	665	222	11640	52.2 ± 27.1	73
149687	SRDL	26/06/2015	26/12/2015	547	183	11181	60.8 ± 24.8	66
149688	SRDL	08/07/2015	14/04/2016	844	281	11066	39.2 ± 21.2	87
149689	SRDL	24/06/2015	20/12/2015	537	179	12746	70.8 ± 34.6	75
Mean ± SD				655 ± 429	174 ± 52	8577 ± 2842	49.1 ± 9.8	85 ± 17

To assess the effect of horizontal physical gradients on the foraging behaviour of leatherback turtles (associated with HRT areas), we extracted at each turtle location the associated SST and SSH from the *Global sea physical analysis and forecast* product (PHYS 001–024) at a resolution of 0.08 ° (from U.E Copernicus Marine Service Information). We then calculated the values of SST gradient (SSTgrad) and SSH gradient (SSHgrad) at the locations of each turtle. We then used the areas with the highest SSTgrad and SSHgrad magnitude (≥ quantile 0.95) to identify the locations of oceanic fronts. Then we assessed the use of frontal zones by leatherback turtles based on the distance to the closest frontal zone identified. We repeated the analysis to determine whether the turtles directly targeted SST fronts or if they were attracted by another oceanographic feature present at frontal regions. This procedure used *Finite-Size Lyapunov Exponents* (FSLE, D'Ovidio et al., 2004) and focused on pure transport diagnostics. The FSLE method provides a direct measurement of local stirring by sub-mesoscale currents, and the separation of waters coming from different regions by the FSLE ridges makes it possible to identify water masses with different physical properties (D'Ovidio et al., 2010; De Monte et al., 2012). FSLE diagnostics were computed as described in Bon et al. (2015) and the FSLE diagnostics were extracted at each turtle location at a 0.08 ° horizontal resolution. For the SST and SSH fronts, the distance to the closest FSLE filament with a gradient magnitude ≥ quantile 0.95 was then calculated for each turtle location.

2.7.2. *Vertical variables*

We assessed the habitat use of leatherback turtles in the vertical dimension by extracting sea water temperature, sea water salinity, mixed layer depth (MLD) and sea water chlorophyll *a* concentration from Copernicus Marine Service Information. These parameters were extracted at each dive location and for each maximum depth reached by all turtles equipped in 2015. The use of vertical habitat by the turtle equipped in 2014 could not be characterized due to the coarse resolution of the diving data (only 1 maximum dive depth per location). We extracted temperature, salinity and MLD (using Kara et al.'s method (2000a)) data from June 2015 to April in 2016 from the *Global physical analysis and coupled system forecast* product (PHY 001–015), available from Copernicus, at a 0.25 ° horizontal resolution and depths of 0–400 m. Similarly, we extracted sea water chlorophyll *a* concentration data from the BIO 001–014 product at a 0.5 ° horizontal resolution and depths of 0–400 m. We then used these data to locate the thermocline, halocline and nutricline depths. The seasonal thermocline was defined as the layer comprised between the MLD (upper layer of the thermocline) and the maximum MLD during the previous winter peak below (e.g. lower layer, in February 2015 for the tags deployed in June 2015). We also estimated the halocline and nutricline depths of each dive location from the salinity and chlorophyll *a* gradients, respectively.

2.8. *Diving behaviour analysis*

An indication of dive shape was obtained through the Time of Allocation at Depth (TAD) index, calculated by using the four inflection points of the summarized profiles provided by SRDL tags deployed in 2015. We used Fedak et al.'s method (2001) to calculate the TAD and thus estimate the type of activity the turtles displayed during the dives. Exploratory dives commonly corresponded to V-shaped dives with $0.5 \leq$ TAD < 0.75, and foraging activity at the bottom of the dive corresponded to U-shaped dives with $0.75 \leq$ TAD<1. We fixed the average rate of change of depth at 1.4 m s^{-1}, as values above this speed are considered biologically unreliable.

3. Results

3.1. *Migratory routes and high residence time (HRT) areas*

The tracked turtles measured (mean ± SD) 160 ± 8.1 cm in curved carapace length, 116 ± 6.4 cm in curved carapace width and 206 ± 13.7 cm in circumference. We obtained 655 ± 429 (mean ± SD) locations per turtle, for a tracking duration ranging from 99 (#149680) to 281 days (#149688, Table 1). The total distance travelled varied from 4957 km (#149680) to 12746 km (#149689, mean ± SD: 8577 ± 2842 km). The actual daily speed (corrected for oceanic currents) ranged from 39.2 ± 21.2 to 70.8 ± 34.6 km d^{-1} (#149688 vs. #149689, respectively, mean ± SD: 49.1 ± 9.8 km d^{-1}). The average elapsed time to reach the HRT areas (putative foraging grounds) was 85 ± 17 d (mean ± SD; range: 65–115 d, #149680 vs. #149684, respectively).

The 10 females tracked in this study left French Guiana between late June and late August, and occupied HRT areas between August and November. They headed in various directions towards mid-latitude areas, i.e. south-eastern US continental shelf, Newfoundland-Labrador, the Azores or even pelagic waters in the North Atlantic (Fig. 1a). The areas that were identified as putative foraging grounds based on a HRT were spread between 30–45 °N, and were located either in neritic or pelagic zones. Three turtles used a coastal HRT area located off the shores of the south-eastern US shelf (#149680, #149682 and #149689). Another (#149687) remained in the neritic HRT area of Newfoundland-Labrador, at the mouth of the Saint Lawrence River, and the six remaining turtles spent most of their time in pelagic waters. The running circle providing the best contrast in terms of residence time series analysis had a radius of 80 km. The largest HRT percentage was observed from October (n=10) to December (n=8) (Fig. 1b).

3.2. *Associations with biological features*

The initial part of the migration within the core of the North Atlantic subtropical gyre corresponded to low RT (hereafter 'transit

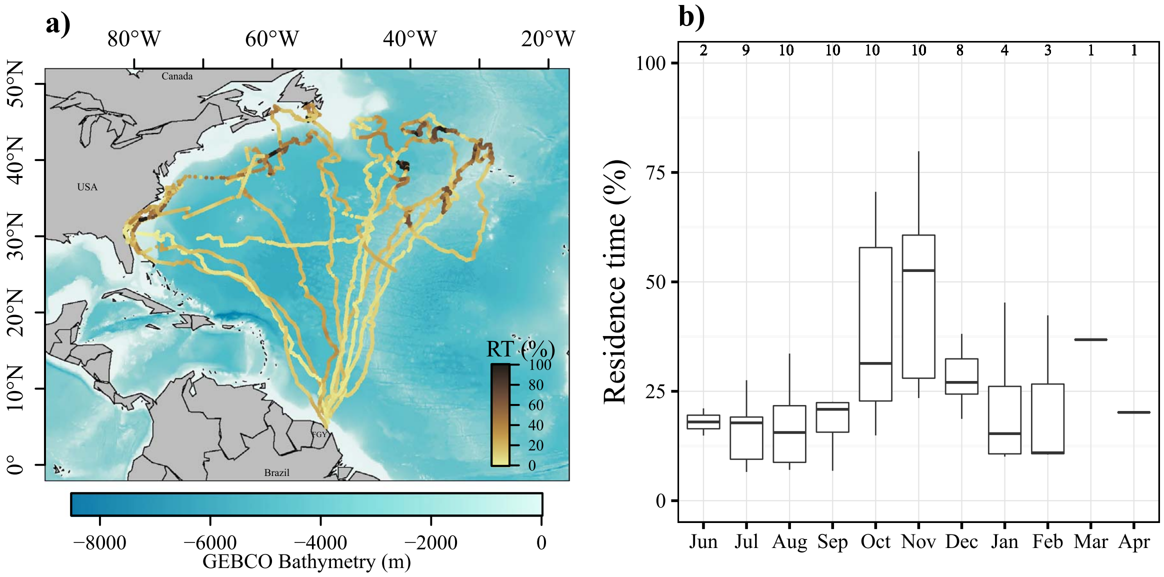

Fig. 1. (a) Proportion of residence time (RT in %) calculated along the 10 leatherback tracks in 2014 (n=1) and 2015 (n=9) and (b) box plots of RT (in %) according to the months of tracking. The RT (initially expressed in days) was converted into a percentage based on the maximum value obtained for each individual to obtain a comparable scale across individuals. (b) The locations associated with the highest values in (a) were considered to be potential foraging areas. FGY indicates the departure point and tagging site located in French Guiana. The numbers in (b) refer to the sample size of each box plot (i.e. the number of turtles; note that only one turtle was still tracked in March and April).

phase') for all females in scantily productive waters containing low levels of micronekton biomass and chlorophyll *a* concentration (Figs. 2a and 2d). When all the transit phases were taken into account, the micronekton biomass was significantly lower than that found in HRT areas (mean ± SE: 0.56 ± 0.04 vs. 1.31 ± 0.25 g m^{-2}, respectively, Wilcoxon test, V=35, $p < 0.05$, Fig. 3a). Similarly, the chlorophyll *a* concentration was significantly lower at locations where the turtles transited (mean ± SE: 0.18 ± 0.04 vs. 0.53 ± 0.13 mg m^{-3}, respectively, Wilcoxon test, V=28, $p < 0.05$, Fig. 3b).

Locations at higher latitudes (> 30 °N) correspond to areas where the turtles spent most of their migration time, and highly productive waters for both the micronekton biomass and the chlorophyll *a* were recorded (Figs. 2b, 2e and 5b). However, most of the leatherback turtles headed southward on leaving these mid-latitude feeding grounds, remaining in waters of expected high chlorophyll *a* concentration (Fig. 2f) rather than high micronekton biomass (Fig. 2c). The euphotic depth was significantly shallower in HRT areas (mean ± SE: 77.9 ± 3.3 vs. 55.5 ± 4.8 m; Wilcoxon test, V =36, $p < 0.005$) – see Figs. 3c, 2g, 2h, 2i. Waters of shallower euphotic depth were associated with higher latitudes (> 30 °N), where the turtles were assumed to feed intensively (Fig. 2h).

3.3. Associations with physical discontinuities

Our turtles experienced warm waters (~30 °C) when crossing the core of the North Atlantic subtropical gyre (see Fig. 4a). After reaching HRT areas at higher latitudes in November, they remained in cooler waters ranging mainly between 15 and 23 °C (Fig. 4b). At the beginning of winter (January), the cold waters coming from the Labrador Current extended further south and the four remaining turtles tracked at this period tended to follow the 20 °C isotherm southward (Fig. 4c). The SSH and SST were significantly lower when the turtles occupied HRT areas (mean ± SE: 9.4 ± 2.8 vs. −14.1 ± 3.4 cm; Wilcoxon test, V=55, $p < 0.005$, Figs. 3g, 4d, 4e, 4f, and mean ± SE: 25.7 ± 0.5 vs. 20.5 ± 1.2 °C; Wilcoxon test, V=55, $p < 0.005$, Fig. 3h, respectively).

During the first and final parts of the migration, corresponding to the low RT phases, the turtles crossed waters associated with low horizontal gradients (SST and SSH fronts), as illustrated in Figs. 6a, 6c, 6d and 6f. They crossed waters associated with low FSLE (Figs. 6g and 6i). In contrast, they remained close to stronger SSH and SST gradients while occupying HRT areas at mid-latitudes (Figs. 6b and 6e). The SST gradient was up to three times higher when on HRT areas (mean ± SE: 0.01 ± 0.002 vs. 0.03 ± 0.006 °C km^{-1}, Wilcoxon test, V=1, $p < 0.01$) - see Figs. 6a, 6b and 6c. The SSH gradient was up to twice as high when the turtles occupied HRT areas (mean ± SE: 0.14 ± 0.01 vs. 0.25 ± 0.05 cm km^{-1}, Wilcoxon test, V=1, $p < 0.05$) - see Figs. 6d, 6e and 6f. The distance to the SST front was significantly shorter when the turtles were in HRT areas than when they were on low RT areas (mean ± SE: 379 ± 32 vs. 37 ± 7.5 km; Wilcoxon test, V=55, $p < 0.005$) – see Figs. 3d and 5c. Similarly, the distance to the SSH front was significantly shorter when the turtles were in HRT areas (mean ± SE: 474 ± 44 vs. 86 ± 22 km, Wilcoxon test, V=55, $p < 0.005$) – see Figs. 3e and 5d). However, the FSLE was not significantly higher when the turtles occupied HRT areas (mean ± SE: 0.13 ± 0.02 vs. 0.21 ± 0.05 $days^{-1}$, Wilcoxon test, V=4, p=0.1094) - see Figs. 6g, 6h and 6i. The distance to the FSLE (filaments) was significantly shorter when the turtles were in HRT areas (mean ± SE: 253 ± 34 vs. 64 ± 22 km; Wilcoxon test, V=54, $p < 0.005$) – see Figs. 3f and 5e.

3.4. Diving behaviour and vertical structures

3.4.1. Turtle maximum depth and dive duration

The Argos-GPS tag recorded 4539 depths and 4614 dive durations. Among the 720 summarized dives transmitted (the tags have not recorded the dives continuously) by the 9 SRDL, on average 80 ± 33 dives per individual were transmitted (range: 41–137 dives per turtle, #149680 vs. 149688). Over the 10 tags, 27% of the dives were less than 10 m deep (Fig. 7a). Maximum dive depths were significantly different between individuals (Kruskal-Wallis rank sum test, χ^2=49, $p < 0.001$). The turtles dove significantly deeper when occupying low RT areas (mean ± SE: 82.4 ± 5.6 vs. 38.5 ± 7.9 m, Wilcoxon test, V=55, $p < 0.005$) – see Fig. 7a. Dive durations varied from 0.5 to 85 min, with 26% of the dives lasting less than 10 min, and 31% between 20 and 45 min (Fig. 7b). Dive durations differed significantly between individuals (Kruskal-Wallis rank sum test, χ^2=57, $p < 0.001$). The turtles performed longer dives when in low RT areas (mean ± SE: 27.0 ± 1.3 vs. 14.3 ± 2.4 min, Wilcoxon test, V=54, $p < 0.005$) – see Fig. 7b.

3.4.2. Surface interval and TAD

Among the 720 dives recorded by the SRDL tags, 76% of the surface intervals lasted less than 5 min (mean ± SE: 13.1 ± 2.4 min). Surface

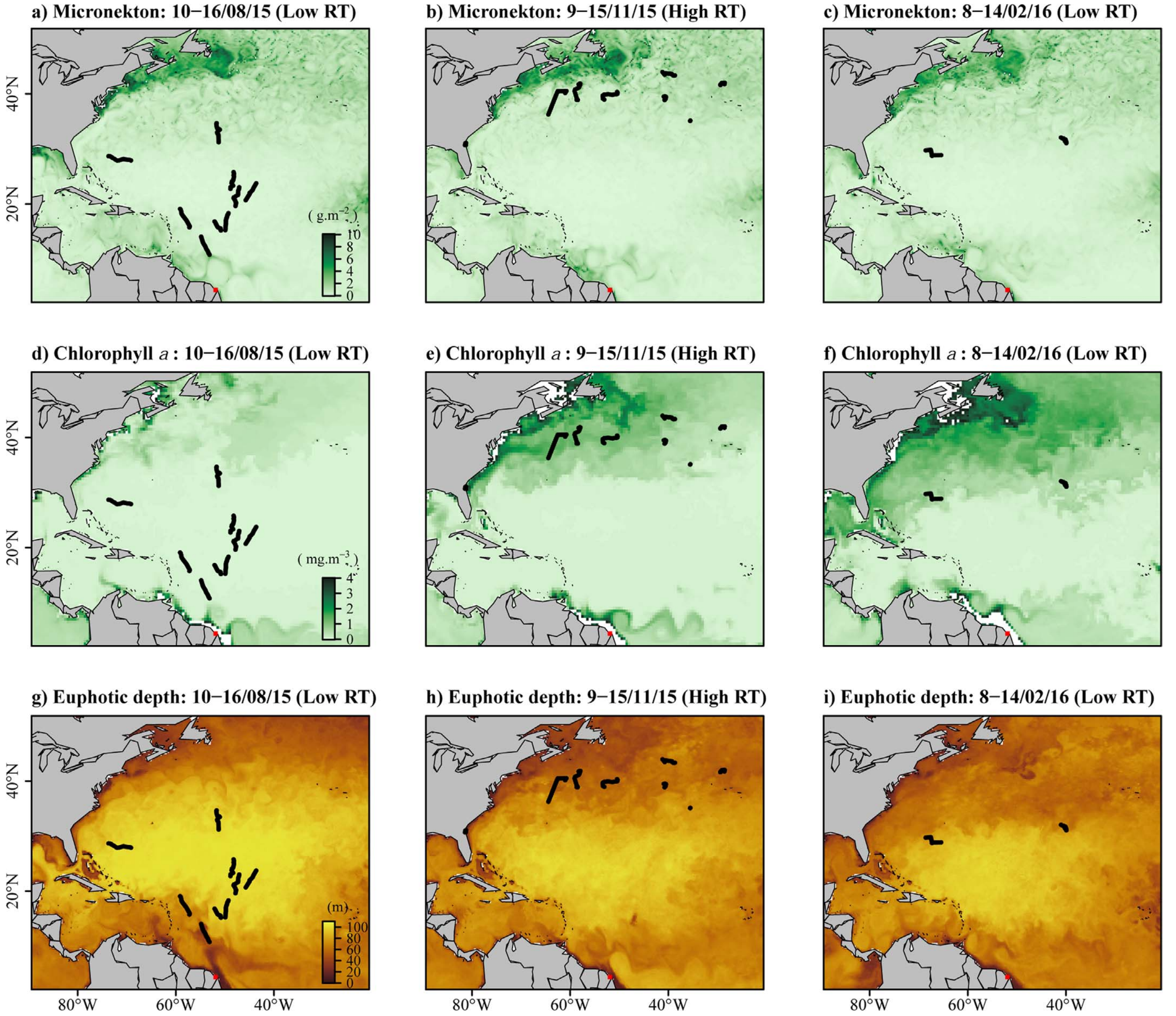

Fig. 2. Maps of the weekly averaged micronekton biomass predicted from SEAPODYM (a, b, c), the chlorophyll *a* concentration extracted from Copernicus (d, e, f) and the euphotic depth (g, h, i) predicted by SEAPODYM during three phases: the crossing of the North Atlantic gyre (a, d, g: low RT, *n*=10), the high RT period at mid-latitudes (b, e, h, *n*=10) and after leaving the high RT areas (c, f, i, *n*=3). The black dots correspond to the locations of the leatherback turtles tracked from French Guiana for the corresponding week and the red square to the migration starting point. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

intervals recorded by the 9 SRDL tags differed significantly between individuals (Kruskal-Wallis rank sum test, χ^2=68, $p < 0.001$) but did not differ significantly according to the type of behaviour (mean ± SE: 12.9 ± 2.6 vs. 11.3 ± 2.6 min, Wilcoxon test, V=18, p=0.6523). The Time of Allocation at Depth (TAD) varied from 0.25 to 0.92 and was on average (± SE) 0.59 ± 0.004. With a TAD below 0.5, 11% of the 720 dives recorded by the SRDL tags could not be assigned to a U or V dive shape, whereas 85% corresponded to V-shaped dives and 4% to U-shaped dives.

3.4.3. SST and temperature at turtle maximum depth

The values for SST and temperature at the maximum recorded depth of each turtle decreased over the tracking period, with the highest values recorded during the first month of tracking in June (mean ± SE: 28.1 ± 0.3 and 27.6 ± 0.1 °C, SST and temperature at maximum dive depth respectively) and the lowest in November (mean ± SE: 21.1 ± 3.1 and 20.7 ± 3.1 °C) – see Fig. 8. The difference between SST and temperature at maximum depth varied between 0 to 6.2 °C, and was at its highest in July (mean ± SE: 3.6 ± 1.4 °C) and lowest in February (0.09 ± 0.1 °C). This smaller difference between SST and temperature at maximum depth coincides with the strong deepening of the mixed layer from October to February (Fig. 8).

3.4.4. Mixed layer depth and thermocline

The deepness of the mixed layer at turtles' locations increased substantially between August and November (mean ± SE: 31.6 ± 10.7 vs. 96.1+49.7 m) – see Figs. 8 and 9. The lower limit of the thermocline also deepened from June (9.4 m, n=2) to November (mean ± SE: 260.3 ± 121.7 m, n=8), then became slightly shallower (February mean ± SE: 175.5 ± 43.3 m, n=3). The turtles remained above it while occupying HRT areas (from October). Before reaching HRT areas (June to October), the turtles dived mainly below the mixed layer (Fig. 9). Afterwards, they performed shallower dives from October to February, remaining within the mixed layer (Fig. 9).

3.4.5. Nutricline and halocline

Turtle maximum dive depth was positively correlated to the vertical

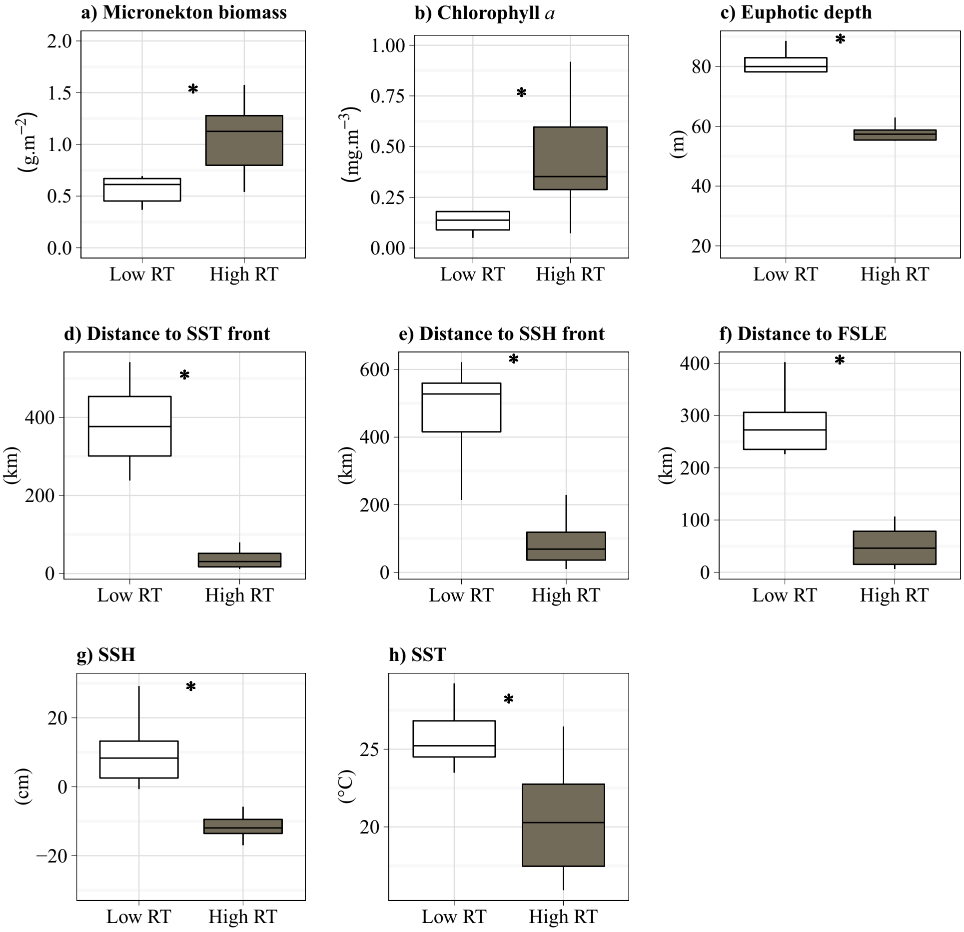

Fig. 3. Box plots of micronekton biomass (a), chlorophyll *a* concentration (b), euphotic depth (c), distance to the closest SST front (d), distance to the closest SSH front (e), distance to the closest FSLE filament (f), SSH (g) and SST (h) for both modes (low RT in white and high RT in dark grey). The stars in each plot indicate the significant differences between the two modes for each variable.

chlorophyll *a* gradient magnitude (nutricline depth derived from model forecast, Spearman correlation test: R^2=0.34, $p < 0.001$) and to the depth at which chlorophyll *a* concentration is maximum (Spearman correlation test: R^2=0.41, $p < 0.001$). However, the maximum dive depth reached by the leatherback was not correlated to the magnitude of the vertical salinity gradient (halocline depth derived from model forecast, Spearman correlation test: R^2=−0.015, p=0.682).

4. Discussion

The use of satellite tracking together with a set of environmental variables (from remote sensing data and model simulations) in this study allowed us to shed light on the role played by the Gulf Stream frontal system in the selection of areas eliciting high residence times (HRT) by the North Atlantic leatherback turtle.

4.1. Migration across the North Atlantic basin

The movement and diving behaviours of the leatherback turtle have been comprehensively investigated on an international scale over the past decade, with particular attention paid to their migration cycle across the Atlantic Ocean (Bailey et al., 2012b; Eckert et al., 2006b; Fossette et al., 2010b, 2010a; James et al., 2005a, 2005b; Ferraroli et al., 2004; Hays et al., 2004; McMahon and Hays, 2006; López-Mendilaharsu et al., 2009; Dodge et al., 2014). Although numerous studies have been conducted in populations from western French Guiana (Fossette et al., 2008, 2010b, 2010a), the present study is the first to investigate the movements and diving behaviour of individuals from the Eastern population. Despite the genetic differences between the two French Guianese populations (Molfetti et al., 2013), the eastern and western individuals showed similar movement patterns. Indeed, like adult females from the Western population (see Fossette et al., 2010b, 2010a; Ferraroli et al., 2004), our tracked individuals migrated northward to reach relatively higher latitudes (> 30 °N) where they tended to display movement behaviour leading to a local increase in residence time during autumn and winter, in either coastal or pelagic habitats. The HRT spent in some particular areas at mid-latitudes indicate that these areas may correspond to foraging grounds. The importance of these potential foraging grounds for this species is reinforced by previous studies that have already reported same hot-spots for the leatherback in Florida, Nova Scotia and the Azores (Eckert et al., 2006b; Fossette et al., 2010a, 2010b; Ferraroli et al., 2004; James et al., 2006; Hamelin et al., 2014). After occupying HRT areas at mid-latitudes, the two turtles that transmitted data for the longest tracking durations headed back southward. While in high RT areas, these two individuals have experienced low SST reaching up to 12 °C. Despite these occasional SST encountered, for most of our tracked turtles, the thermal barrier seemed to occur between the 15–20 °C SST isotherm while foraging, with 77% of the turtles remaining in warmer water than 15 °C. These findings are in accordance with the 15 °C thermal tolerance suggested by McMahon and Hays (2006) for this species. Indeed, despite their endothermic capacity (James and Mrosovsky, 2004), it has been suggested that temperature thresholds might limit the amount of time the leatherback turtles can spend in some cold water areas (Witt et al., 2007). The relatively short tag life (6 ± 2 months) was however a drawback for this study, which would

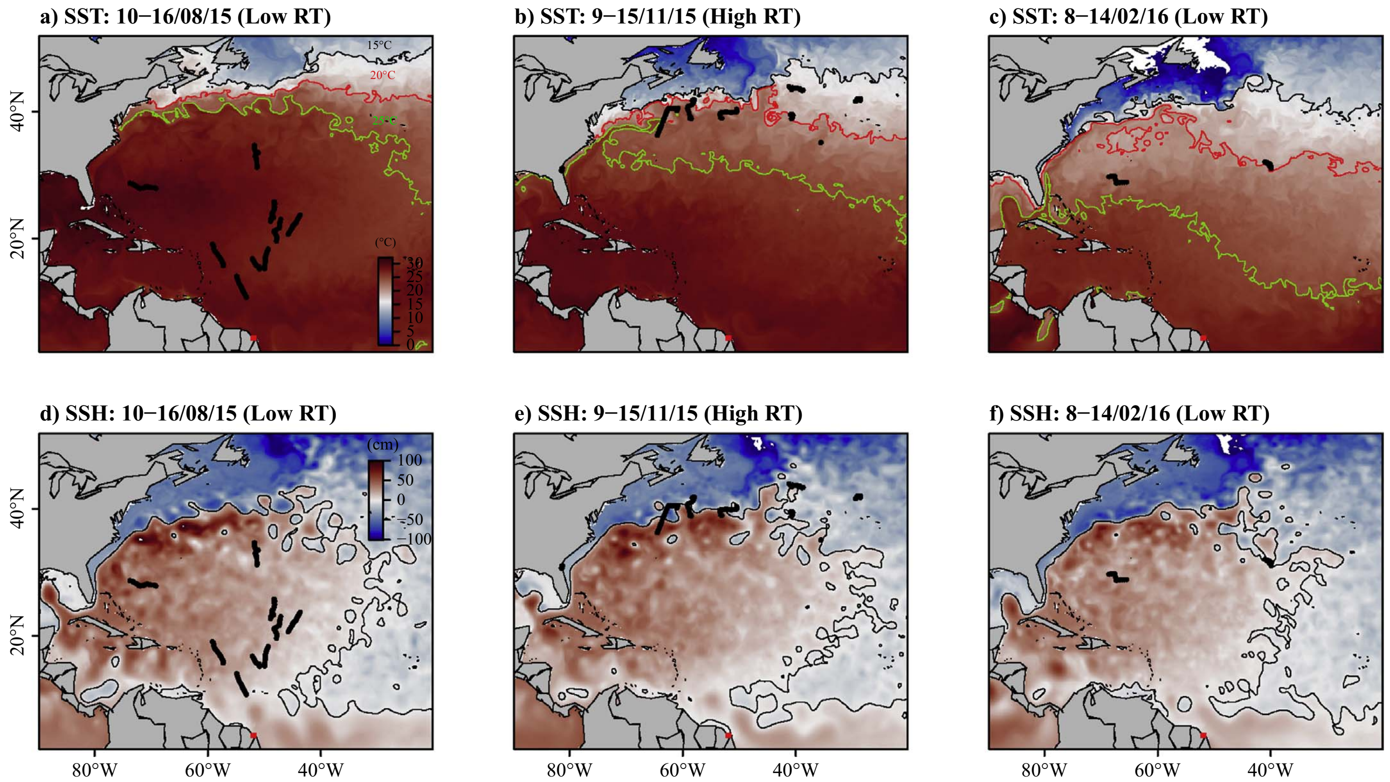

Fig. 4. Maps of the weekly averaged SST (a, b, c) and SSH (d, e, f) derived from Copernicus during three phases: the crossing of the North Atlantic gyre (a, d: low RT, n=10), the high RT period at mid-latitudes (b, e, n=10) and after leaving the high RT areas (c, f, n=3). Three SST contours were superimposed: 15 °C, 20 °C and 25 °C, and the SSH contour (0 cm) refers to the location of the Gulf Stream front. The black dots correspond to the locations of the leatherback turtles tracked from French Guiana for the corresponding week and the red square to the migration starting point. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

require a period of 2–4 years to track the entire remigration cycle across the North Atlantic Basin. There is thus a clear need for further tag deployment to identify the different habitats targeted by this species during post-nesting migration.

4.2. Associations with biological variables

In this study, the leatherback turtles travelled at high speed when crossing the nutrient-poor North Atlantic subtropical gyre, reflecting a transit behaviour. This area is considered as an 'ocean desert' (Tomczak and Godfrey, 2013), due to its scant primary productivity (0.50 mg C m^{-2} d^{-1}, Marañón et al., 2000). In contrast, the turtles spent more time and concentrated searching in HRT areas in the colder waters of upwelling and mid-latitude regions (Marañón et al., 2000), where primary productivity can reach up to 1000 mg C m^{-2} d^{-1}. There is a lack of documentation concerning the spatial distribution of jellyfish (Houghton et al., 2006), but primary production or chlorophyll *a* concentration were evidenced to be good proxies for leatherback prey availability (Fossette et al., 2010a; Dodge et al., 2014). The probability to forage was shown to increase with chlorophyll *a* concentration (up to 2.5 mg m^{-3}) for the Western Pacific (Bailey et al., 2012b) and the North Atlantic populations (Dodge et al., 2014). Similar results were found in our study, where values of chlorophyll *a* on assumed foraging grounds (corresponding to HRT areas) reached concentrations up to three times higher than those recorded in transit areas (0.18 ± 0.04 vs. 0.53 ± 0.13 mg m^{-3}, respectively). Furthermore, a clear match was observed between the high chlorophyll *a* concentrations and the HRTs, evidencing a remarkable synchronization of this species with areas of high productivity in the North Atlantic. However, as chlorophyll *a* concentrations come from forecasting ocean models (Copernicus database), we can observed some discrepancies, such as the subtropical gyres of the North Atlantic that are predicted slightly too oligotrophic, or the overestimation of the chlorophyll *a* in the tropical band. Such differences may lead to misinterpretation of tracking data when looking at fine-scale movements (1–10 s of km). But the purpose of our study was to look at mesoscale patterns (10–100 km) and consider relative chlorophyll *a* values (and not absolute values) to fit the accuracy of our tracking data, making the output of Copernicus model adequate and reliable.

As mentioned by Fossette et al. (2010b), a more reliable picture of jellyfish distribution may be obtained by looking at a higher trophic level than chlorophyll *a* (Strömberg et al., 2009). In this context, SEAPODYM recently appeared as a promising model to provide estimations of the spatio-temporal distribution of micronekton, including cephalopods, crustaceans, fishes and jellyfish (Lehodey et al., 2010). We therefore hypothesized that the micronekton biomass provided by this model would match locations of foraging leatherbacks better than chlorophyll *a*. Although the presence of chlorophyll *a* seemed to better match the occurrence of HRT areas, levels of micronekton at these locations were more than twice higher than those found in low RT areas (0.55 ± 0.04 vs. 1.31 ± 0.25 g m^{-2}). SEAPODYM predictions were based on the maturation time of pelagic organisms, i.e. 1–2 months for zooplankton and 10 months for micronekton (both at 15 °C; Conchon, unpublished data), but the maturation time of jellyfish is shorter than 10 months. This may explain why the concentration of micronekton biomass was not at its highest in HRT areas at mid-latitudes. A further study including the zooplankton output updated from SEAPODYM may nevertheless provide a better explanation for the habitat selection by leatherbacks.

4.3. Associations with physical discontinuities

The Eastern French Guianese leatherback turtles we tracked tended to display HRT behaviour mainly along physical discontinuities at mid-latitudes (> 30 °N), probably because such interfaces correspond to nutrient-rich waters where jellyfish aggregate (Sims and Quayle, 1998; Greer et al., 2013; Powell and Ohman, 2015). At the northern edge of the Gulf Stream, its warm waters meet the cold Labrador Current

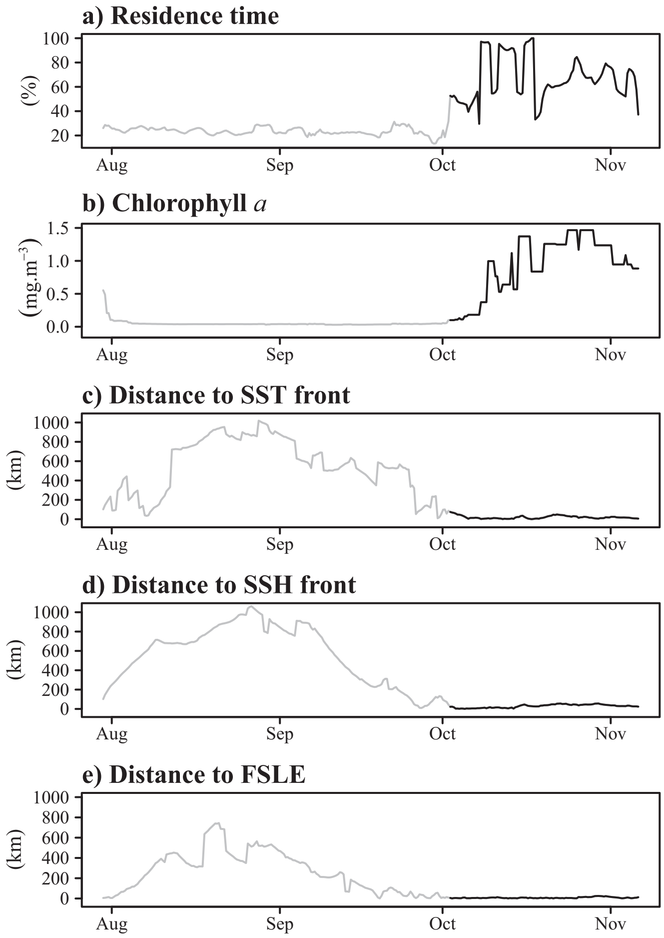

Fig. 5. Proportion of RT (a, in %) and four environmental variables (b, c, d, e) extracted along the track of turtle #149680, namely: chlorophyll *a* concentration (b), distance to the closest SST front (c), distance to the closest SSH front (d) and distance to the closest FSLE filament (e). The highest RT values (from October onwards) were considered to be a foraging activity, and the black parts of the lines refer to the putative foraging mode.

waters, creating a sharp temperature gradient in an area referred as the Gulf Stream north wall (GSNW, Sanchez-Franks et al., 2015). The shelf-slope front (SSF), a front located off the northeast coast of the United States and Canada, separates colder, less saline continental shelf waters from warmer and more saline slope waters (Bisagni et al., 2009), where most of our turtles (60%) displayed HRT behaviour. However, the HRT areas of three turtles were located on the shelf waters south of North Carolina-United States, in the South Atlantic Bight, where they used the lower branch of the Gulf Stream, characterized by much less extreme temperature gradients. Our results highlighted a surprising synchronization and aggregation of all the leatherback turtles between these two fronts before migrating back south.

HRT areas tended to occur preferentially along the SST and SSH gradients, as well as along the FSLE filaments. The identification of these frontal zones enabled us to delineate the frontal boundaries of the GSNW and the SSF. The strong association with these physical discontinuities was confirmed by the shorter distance to the closest front (SST gradient, SSH gradient and FSLE filament) while in HRT areas compared to transit periods. Several studies have already described the tendency for some sea turtles species (loggerhead and leatherback) to associate with frontal structures in the Pacific with the Kuroshio Current (Polovina et al., 2004, 2006; Polovina and Howell, 2005; Scales et al., 2015), or in Atlantic Ocean with the Gulf Stream (Eckert et al., 2006b; Fossette et al., 2010a; Lutcavage, 1996; Witherington, 2002). But to date, only one study has demonstrated such affinities between the leatherback movements and the Gulf Stream frontal system using oceanographic data (Dodge et al., 2014), but such findings were limited to the horizontal dimension and true for a limited number of individuals (n=2). The associations with filaments at the sub-mesoscale in our study (identified via FSLE), in agreement with findings in previous studies conducted on penguins (Lowther et al., 2014; Bon et al., 2015; Whitehead et al., 2016) and seals (Nordstrom et al., 2013; Lowther et al., 2014), confirms the importance of frontal areas in the aggregation of prey.

Regions of high FSLE and strong SSH and SST gradients may all provide complementary data facilitating the interpretation of animal tracking (De Monte et al., 2012). Strong SSH gradients correspond to high kinetic energy and high FSLE to confluence/frontal regions, while a strong SST gradient corresponds to frontal regions marked by temperature difference, where upwelling/downwelling can occur. These three diagnostics can diverge in regions of intermediate or weak kinetic energy, where a confluence is the result of the interaction of multiple mesoscale features and of their temporal evolution and in which high SST gradients only occur at certain confluences (D'Ovidio et al., 2013). However, these diagnostics may be strongly correlated in highly energetic and contrasted regions where gradient intensification by the mesoscale currents arises on relative short time scales (i.e. days), and coincide with the occurrence of strong temperature gradients. This is the case for the branch of the Gulf Stream targeted by the turtles in our study, and may explain why the associations with frontal areas are similar in terms of SST gradients, FSLE, and SSH contours.

4.4. *Affinities for vertical structures*

The leatherback turtles we tracked performed shallower dives while in HRT areas (38.5 ± 7.9 m) than during transit (82.4 ± 5.6 m). This is in accordance with the behaviour of individuals of the Western French Guianese population (53.6 ± 33.1 vs. 81.8 ± 56.2 m, Fossette et al., 2010a). This behaviour should enable them to get an easier access to prey, which is assumed to concentrate in the upper layer (Hays et al., 2008). The analysis of residence time data showed that the tracked females started to display HRT behaviour during early autumn (October), when the phytoplankton bloom begins along the GSNW (Friedland et al., 2016) and the phytoplankton net growth rate increases in the subarctic Atlantic waters located further north (> 40 °N, Behrenfeld, 2010). We equipped our turtles at the nesting peak in June to obtain a reliable picture of the population trend. Despite the low light conditions in the North Atlantic during autumn and winter, the deep winter mixing of the upper layer favours the phytoplankton bloom formation via biomass accumulation (Behrenfeld, 2010). During low stratification months (October-May) in the South Atlantic Bight, where three turtles spent most of their time, the winds and small temperature differences between nutrient-rich water intrusions and the overlaying cold waters bring subsurface nutrient intrusions to the upper layers, as well as cold air outbreaks, favouring the frequent vertical redistribution of chlorophyll *a* and therefore avoiding nutrient depletion in this region (Martins and Pelegrí, 2006).

As our turtles performed mostly shallow dives while in HRT areas at mid-latitudes, the depths they reached during this period were mainly within the mixed layer. In the North Atlantic, the deepest mixed layer occurs between January and May during deep water formation at ~40 °N (Kara et al., 2003). The mixed layer started deepening in October at locations further south (30–40 °N) where the turtles aggregated, coinciding with the period when the turtles started performing shallower dives. The turtles remained within this mixed layer while in HRT areas over the winter period (n=4 in January to n=1 in April). A similar behaviour was observed by Fossette et al. (2010a) for the Eastern French Guianese leatherback turtles, and could be performed to get an easier access to their prey by maximizing energy gain while foraging. Reaching shallower depths while in HRT areas may also reflect the distribution of jellyfish, which is known to be more abundant in the upper layer in cold waters (Longhurst et al., 1995).

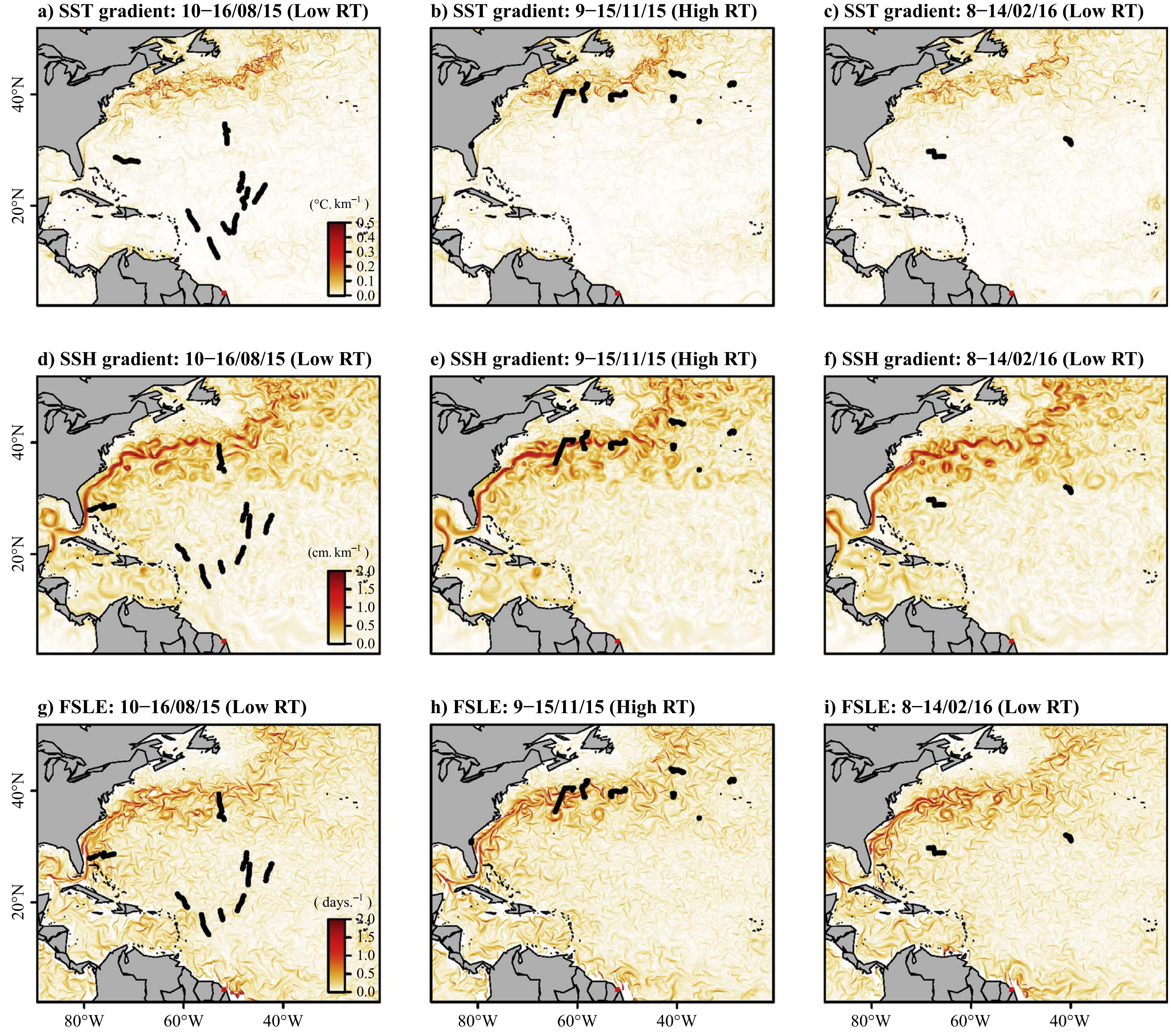

Fig. 6. Maps of the weekly averaged SST gradient (a, b, c), SSH gradient (d, e, f) and FSLE (g, h, i) during three phases: the crossing of the North Atlantic gyre (a, d, g: low RT, n=10), the high RT period at mid-latitudes (b, e, h, n=10) and after leaving the high RT areas (c, f, i, n=3). The oceanic frontal zones were associated with the highest values of the three gradients. The black dots correspond to the locations of the leatherback turtles tracked from French Guiana for the corresponding week and the red square to the migration starting point. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

This deep mixed layer, associated with high nutrient biomass, may therefore explain the remarkable aggregation of leatherback turtles at higher latitudes during autumn and winter. Although the deepest mixed layer commonly occurs during winter, it occurs during the austral autumn in the southern hemisphere in the Western Australia and coincides with high values of chlorophyll a (Rousseaux et al., 2012), thus enabling the replenishment of the surface waters via vertical mixing. The turtles in our study remained within the mixed layer while in HRT areas (i.e. above the upper limit of the thermocline) and dove below it while in other areas, and did not show any particular association with the thermocline or any other strong vertical gradient area (halocline or nutricline), contrary to findings in previous studies conducted on fur seals (Nordstrom et al., 2013), Atlantic olive ridleys (Chambault et al., 2016) and Atlantic leatherback turtles (Bailey et al., 2012a; Hamelin et al., 2014). This difference may be explained by the methodology used to calculate the vertical gradients: the thermocline is commonly defined based on the temperature gradient magnitude (Bailey et al., 2012a), but this approach can be biased by incomplete temperature profiles (over the continental shelf) or insufficient depths reached by the individuals. To avoid a possibly biased identification of the thermocline depth, we decided to use the MLD provided by Copernicus as the upper limit, and the deepest mixed layer during the previous winter peak for the lower limit. In contrast, Hamelin et al. (2014) used *in situ* temperatures provided by CTD tags to determine the thermocline, which probably resulted in less errors and a better resolution than when using the outputs from ocean forecasts such as Copernicus.

In the North Atlantic, the breakdown of the seasonal thermocline under the effects of storms and winds during autumn leads to deep mixed layer that generates a quasi-uniform layer of temperature (isothermal layer) throughout the water column, with relatively homogeneous values between the upper layer of the thermocline and the surface (Lentz et al., 2003). Unlike the cooler SST encountered when performing HRT behaviour (20.0 ± 3.9 °C, range: 15.9–26.3 °C), the

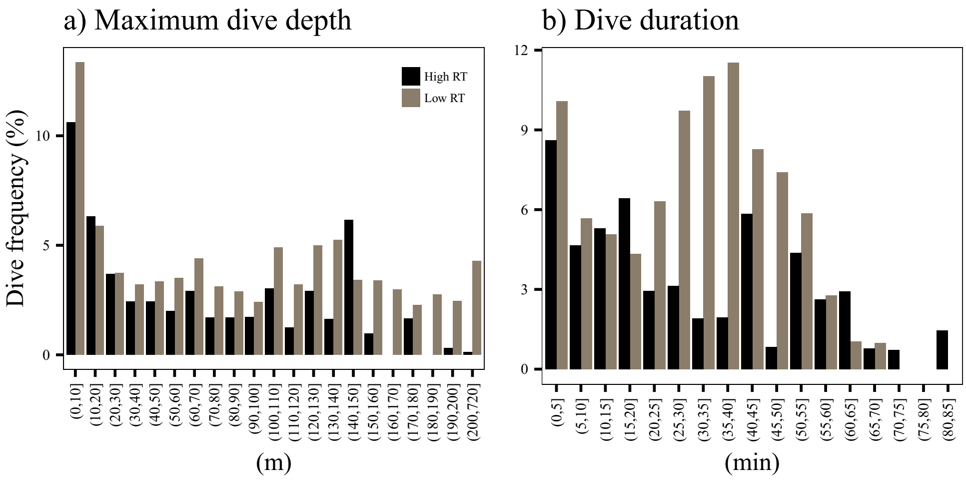

Fig. 7. Histograms of the maximum dive depth (a) and the dive duration (b) for the 10 tags deployed in 2014 (*n*=1) and 2015 (*n*=9) and for both modes (low RT in grey vs. high RT in black).

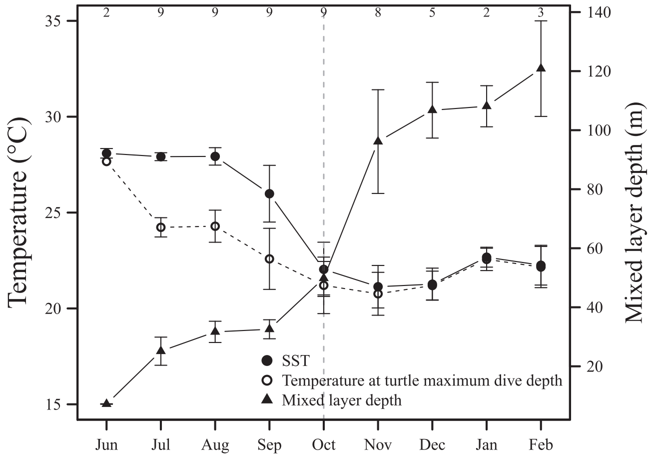

Fig. 8. Monthly mean (± SE) of SST (filled dots), *in situ* temperature at the turtle maximum dive depth (empty dots) and mixed layer depth (triangles) extracted for the 9 SRDL tags and from Copernicus database. The vertical dotted line refers to the beginning of the high RT period for the majority of the turtles. The numbers refer to the sample size of each box plot (i.e. the number of turtles).

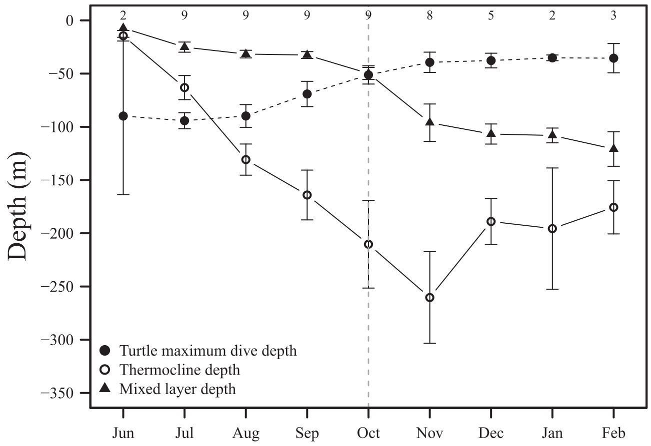

Fig. 9. Monthly mean (± SE) of turtle maximum dive depth (filled dots), lower limit of the thermocline (empty dots) and mixed layer depth (triangles) extracted for the 9 SRDL tags. The lower limit of the thermocline and the mixed layer depth were extracted from the Copernicus database. The vertical dotted line refers to the beginning of the high RT period for the majority of the turtles. The numbers refer to the sample size of each box plot (i.e. the number of turtles).

turtles experienced warm SST during their transit across the subtropical gyre (28.1 ± 1.8 °C, range: 20.9–30.9 °C). Besides the SST difference between the two movement modes, there was also a significant temperature difference of up to 4.2 °C between the surface and the maximum dive depth within the gyre. While crossing the gyre, the females therefore experienced shallow mixed layer and warm temperatures. As Fossette et al. (2010a) found for the western French Guianese population, our eastern French Guianese turtles performed deep dives (104 ± 80.7 m) in this nutrient-poor area (Marañón et al., 2000; Strömberg et al., 2009), which may indicate that they targeted cooler temperatures in deeper layers to save energy during the transit phase of their migration. The selection by these turtles of HRT areas located at mid-latitudes suggests a preference for cool waters (mean temperature at maximum depth: 19.1 ± 4.9 °C), as observed in leatherbacks from the East Pacific population (Bailey et al., 2012b). The long post-dive surface intervals (13.1 ± 2.4 min) observed in our study reinforce the hypothesis that some individuals may swim at the surface to process and eat large prey items in the Northwest Atlantic (James and Mrosovsky, 2004). The deployment of 3D-acceleration data loggers together with cameras should make it possible to identify prey catch attempts during the dives, and therefore relate this activity to leatherback diving behaviour. Despite the relatively low number of dives recorded by the 9 SRDL tags (*n*=720), the 4614 dives collected by the Argos-GPS tag provide complementary dive data to support the first evidence of the use of the mixed layer by the adult female leatherback turtles during post-nesting migration across the North Atlantic. While in high RT areas, the shallower diving behaviour of the turtles (within the first 55 m) was already evidenced by a previous study (Fossette et al., 2010b), which therefore reinforces the observed pattern of the turtles remaining mainly within the deep mixed layer. In a lesser extent, the low number of dives recorded could however prevent from observing some occasional deep dives performed below the mixed layer. To cope with this limitation, some additional SRDL tags programmed to collect several daily profiles need to be further deployed. The deployment of additional tags over longer periods (at least one year) is required to collect complementary data on both the horizontal and vertical movements, since leatherback behaviour shows inter-annual variability.

5. Conclusion

The present study is the first to document the post-nesting migration movements of the Eastern French Guianese population of leatherback turtles. Our findings highlight the crucial role of the Gulf Stream front in the selection of potential foraging habitats by this species. The use of innovative and 3D ocean models for estimating SSH, temperature, salinity, chlorophyll *a*, FSLE (computed from satellite-derived currents), and micronekton biomass (from SEAPODYM) enabled us to investigate the link between leatherback movements and frontal structures in both the horizontal and vertical dimensions. Although the high residence time areas of the turtles were geographically remote (spread between 80–30 °W and 28–45 °N), these probable foraging grounds were all found in close proximity to the Gulf Stream frontal zone, a highly dynamic and productive physical discontinuity separating the warm and salty waters of the Gulf Stream from the cold and less-saline waters of the Labrador Current. As seen in other oceanic fronts, this extensive area is known to enhance primary production and thus aggregate low trophic level organisms such as jellyfish, which is the main food resource for leatherback turtles. In a context of climate change, anticipating the evolution of such frontal structure under the influence of global warming is crucial to ensure the conservation of this vulnerable species.

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ANNEXE H

Multidirectional migratory routes of immature green turtles reveal connecting paths between juvenile and adult habitats

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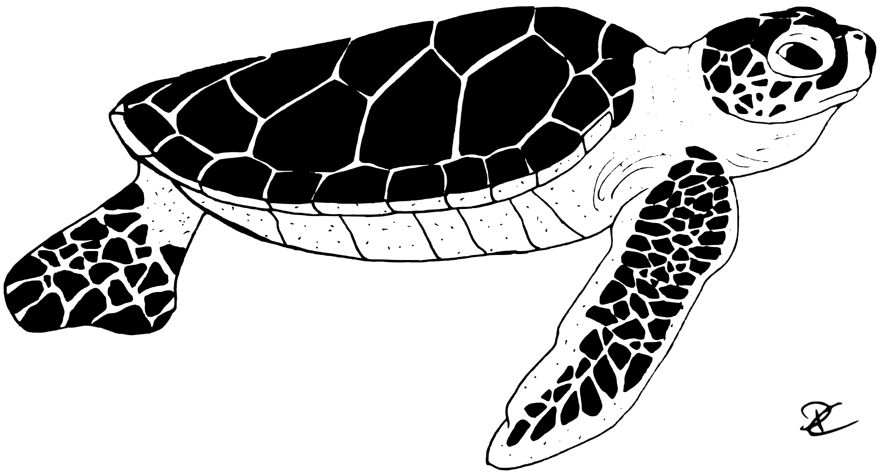

Multidirectional migratory routes of immature green turtles reveal connecting paths between juvenile and adult habitats

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Abstract

While satellite telemetry has made it possible to quantify the home ranges of immature green turtles at different locations in the Caribbean-Atlantic region, little is known about their developmental migration and the connecting paths between immature and adult habitats, especially in the French West Indies (territory including the French islands of Guadeloupe and Martinique). This study aims to identify the migratory routes and transitory hotspots used by immature green turtles from Martinique during their developmental migrations across the Caribbean-Atlantic region. Among the 12 turtles equipped, 9 turtles left Martinique, heading across the Caribbean-Atlantic region in six different directions. The extensive movements of the migrant turtles evidenced the different pathways used during their multidirectional migrations, crossing international waters and more than 25 exclusive economic zones. This confirms the need for an international cooperative network and the provision of up-to-date tracking data to improve the design of Regional Management Units at the pan-Atlantic scale to preserve future breeders found in this extensive area.

Keywords

Chelonia mydas; migration routes; immature green turtle; satellite tracking

1. Introduction

Satellite tracking was recently used to follow the direct movements of juvenile green turtles in the Caribbean-Atlantic region, both within their developmental habitats and during their migration, including their passage through territorial waters. While satellite telemetry has made it possible to quantify the home ranges of immature green turtles at different locations in the Caribbean-Atlantic region (González Carman et al., 2012; Hart and Fujisaki, 2010; Makowski et al., 2005; Meylan et al., 2011), little is known about their migration and the connecting paths between immature and adult habitats, especially in the French West Indies (territory including the French islands of Guadeloupe and Martinique). Using genetic analyses, Bass et al. (2006) demonstrated the high genetic diversity of the immature green turtle population inhabiting Florida developmental waters, i.e. 80% from Costa Rica, 14% from Aves Island, 5% from the United States and 1% from Ascension-Guinea Bissau (Bass and Witzell, 2000). High genetic diversity is also apparent in immature green turtles from Barbados, as they originate from multiple rookeries across the Caribbean region (Luke et al., 2003). These genetic studies are the only ones that attempt to link the developmental migration of immature green turtles from the Caribbean to adult home ranges, making our use of satellite telemetry an innovating approach.

The green turtle is an endangered species on the IUCN red list (Seminoff et al., 2002), and is listed in Appendix 1 of the Washington Convention. This species faces many threats (natural and anthropogenic), including the degradation of marine and nesting habitats, poaching (Wallace et al., 2013) and bycatch (Garcia et al., 2003; Koch et al., 2006; Seminoff et al., 2002; Wallace et al., 2013). In the French West Indies, this species was overexploited for its flesh and its eggs for 500 years (Chevalier, 2005). Three decrees (in 1991, 1993 and 2005) were passed to counter the population decline. The French Ministry for Ecology, Sustainable Development and Energy reinforced these measures by making *Chelonia mydas* a priority species of the restoration plan for sea turtles of the French West Indies (RPSTWI). One of the main objectives of this plan was to study the distribution of immature green turtles using satellite telemetry.

Although juvenile green turtles have been tracked through the Caribbean since the 2000s (Godley et al., 2003; Hart and Fujisaki, 2010; Makowski et al., 2005; Meylan et al., 2011), there is still no data available for immature green turtles located in Martinique. To fill this gap in our knowledge, we tracked 12 immature green turtles tagged in Martinique (Fig. 1). By tracking their movements during developmental migrations, the present study should provide a solid basis for the adequate protection of this species and encourage the development of an international network across the Caribbean-Atlantic region, within the so-called "Atlantic South Caribbean" Regional Management Unit (Wallace et al. 2010).

2. Methods

2.1 Animal capture and tagging

Between 01-05/06/2015, nine immature green turtles were captured by freedivers in the Anses d’Arlet (14°30’9.64’’N, 61°5’11.85’’W, Martinique, France). After spotting a static turtle feeding/resting at the bottom, a freediver dived close to the head of the turtle, as discreetly as possible in order to avoid detection. Once close enough, the diver caught the turtle by the pygales plates of the shell (located behind the nuchal), and brought it to the surface. A second diver held the foreflippers and helped to lift the individual into the boat for measurements and tagging. Each turtle was placed in a pen, and standard morphometric data were recorded, i.e. curved carapace length (CCL) and body mass using an electronic dynamometer. Each individual was marked by inserting a Passive Integrated Transponder (PIT) tag in the right triceps. GPS-Satellite Relayed Data Loggers (GPS-SRDL, Sea Mammal Research Unit, University of St. Andrews, Scotland) were then fixed using epoxy resin following Chevallier et al.’s method (Baudouin et al., 2015). Using the same procedure, between 12-16/10/2015, an additional immature green turtle was fitted with an Argos-Fastloc GPS tag (Wildlife Computers Redmond, WA, USA). And between 14-22/10/2016, two individuals were equipped with SPOT tags (Wildlife Computers Redmond, WA, USA).

2.2 Tracking data analysis

Data were downloaded daily via Argos Message Retriever (WC-DAP, Wildlife Computers-Data Analysis Programs). In order to provide optimum location accuracy and increase the number of positions available to counterbalance errors caused by the proximity to the shore, the 9 GPS-SRDL tags were programmed to simultaneously record Argos and GPS locations. The GPS sampling interval was set to 15 min. Tag position estimates (Argos data) were enhanced by applying a Kalman-filtering algorithm to account for Argos error (CLS, Collecte Localisation Satellites, Toulouse, France).

The proximity to the shore and the possible Argos error resulted in 51% of the positions being found on land after applying the Kalman filter. We used the altimetry product provided by the Hydrographic and Oceanographic Service of the French Navy (SHOM) at a 25 m² resolution to identify these erroneous locations and discard them. Positions associated with a travel speed of over 10 km.h^{-1} were discarded (8%), and also those associated with location class Z (0.1%), considered insufficiently accurate.

3. Results

3.1 General tracking data

Among the 12 immature turtles tracked, 9 left Martinique to perform their migration across the Caribbean-Atlantic region (#149691, #149692, #149693, #149694, #149696, #149697, #150122, #164547 and #164548). The tag instruments transmitted on average 393±179 locations (range: 163 to 618, #149691 vs. #164548 respectively). The length of these migrant individuals varied from 81 to 88.5 cm (mean: 84.3±3.5 cm, #149691 vs. #164548, respectively) and their body mass from 66.4-81.4 kg (mean: 72.8±6.7 kg, #150122 vs. #149691, respectively). The tracking duration was on average 168±82.6 d and the total distance travelled ranged from 1324 km (#149697) to 8771 km (#149696) – see Table 1.

3.2 Migratory routes

The nine individuals headed in six different directions, and two reached a possible conclusive destination (#149694 and #149697, Figs. 1e and 1g). Turtles #150122 and #149691 migrated south-westward (Figs. 1a and 1b). After stopping emitting for a month (probably due to transmission issues or the short surfacing behaviour of green turtles), the tag #149691 transmitted again, indicating that the individual was swimming along the coast of Jamaica as far as until the Caiman Islands, while the tag #150122 followed the Colombian coast towards Costa Rica (Fig. 1a). Turtles #149692 and #149693 migrated south-eastward to reach the Guyana coast (Figs. 1c and 1d). After remaining around the French West Indies for approximately 50 days, these two tags stopped transmitting over the Amazon River plume. Turtle #149694 left Martinique immediately and headed north-westward to reach Florida, which could be considered her final destination as she remained there for at least one week (Fig. 1e). The turtle #149696 left the Surinamese coast to head eastward towards the African coast, probably benefiting from the Equatorial Counter-Current (Figs. 1f and 2). Turtle #149697 remained close to Martinique Island during ~ 3 months before travelling towards Antigua and Barbuda (Fig. 1g). Then she reached the US Virgin Islands, where she remained for several weeks. And the last two turtles (#164547 and #164548) reached the known foraging grounds off the State of Ceará in Brazil (Figs. 1h and

1i). During the tracking duration, the five individuals crossed around 25 territorial waters across the Caribbean-Atlantic region (Figs. 1 and 2).

4. Discussion

This study made it possible to identify transitory hotspots of immature green turtles across the Caribbean-Atlantic region. These newly identified areas require particular attention to ensure the renewal of future generations of breeding green turtles. Prior to our study, there was very little information on the movements of immature green turtles in the Caribbean, and particularly for developmental migrations. Our findings provide existing literature with a new element by identifying the key migratory pathways of juvenile green turtles and presenting new hypotheses on the potential connecting pathways between juvenile and adult habitats, from the Caribbean up to the African coast (Fig. 2).

The morphometric data of these migrant turtles (CCL: 84.3±3.5 cm, body mass: 72.8±6.7 kg) were close to those found by Meylan et al. (2011), who performed a series of laparoscopies (examination of the gonads) on immature green turtles in Panama to determine the minimum size at sexual maturity (Meylan et al., 2011). The minimum size found in their study (81.9 cm CCL), is shorter than the average size of the turtles tagged in our study (84.3 cm CCL, range: 81-88.5 cm), suggesting that our migrant individuals were about to reach sexual maturity, and therefore start their migration, either to discover new developmental habitats (Carr et al., 1978), or possibly to directly reach adult foraging or breeding habitats. Although green turtles reach maturity over a wide range of sizes and body masses (Bjorndal et al., 2012), the CCL values measured in Martinique are shorter but close to the minimum size observed in nesting females from different rookeries of the Caribbean: X'cacel (range: 88.5-117.5 cm CCL), Tortuguero (range: 90.3-122.6 cm CCL) and Panama (range: 86.6-112.5 cm CCL, Meylan et al., 1994b, 2011).

The multiple origins of these juvenile turtles in the Caribbean-Atlantic region could be confirmed by the tracks of migrant turtles that headed towards adult habitats (natal rookeries and foraging grounds). Similar behaviour was observed for some immature green turtles in the Indian Ocean; these individuals had shorter CCL than our migrant individuals (73.5±4.9 cm vs. 84.3±3.5 cm), and successfully reached adult foraging areas (Pelletier et al., 2003). Although most of the tags did not transmit locations until the turtles reached their final destination, some assumptions can be made about the trajectories recorded.

Two individuals (#149694 and #149697) headed north-westward, passing by several adult foraging grounds (US Virgin Islands, Antigua and Barbuda, Puerto Rico, Dominican Republic and Bahamas). Turtle #149697 performed a short migration and remained for several weeks in the US Virgin Islands, known to be a famous foraging ground for both juvenile and adult green turtles that feed on *Thalassia testudinum*, the same species that is found in Martinique (Ogden et al., 1983). Despite the availability of these different foraging grounds and rookeries along her route, turtle #149694 stopped at one site in Florida, suggesting that she had targeted a particular area rather than exploring new developmental habitats: after crossing the many rookeries located north of West Palm Beach (Roberts et al., 2014; Shamblin et al., 2014), and the juvenile reef habitats (Stadler et al., 2014), this turtle ended its migration in Biscayne Bay. This site hosts different communities of seagrasses and macroalgae, as well as many megafauna groups, including sea turtles (Lirman et al., 2014). The seagrasses and macroalgae taxa sampled in Biscayne Bay are also similar to those found in the French West Indies, i.e. *Halodule*, *Syringodium* and *Thalassia* (Chevallier et al., 2016; DEAL Guyane and Agence des Aires Marines Protégées, 2013), and they are particularly abundant where this individual spent most of its time, i.e. near Manatee Bay (Lirman et al., 2014).

Two other turtles migrated south-westward (#149691 and #150122), towards the Venezuelan and Panama coasts respectively. After one month with no location, the tag of turtle #149691 started transmitting again once the individual had crossed the Venezuelan coast, indicating that this turtle was heading for Honduras, possibly targeting either the Honduras nesting site or other adult habitats located in the Gulf of Mexico. Turtle #150122 followed the Panama coast, targeting either the Panama foraging ground or the Costa Rica rookery (Troëng and Rankin, 2005) – see Fig. 2.

Four turtles (#149692, #149693, #164547 and #164548) headed south-eastward, possibly towards the Brazilian foraging grounds used by both adults coming from French Guiana (Baudouin et al., 2015; Chambault et al., 2015) and juveniles (Godley et al., 2003; Lima et al., 1999; Lum et al., 1998). These results confirm the significant contribution of the French Guianan rookery to genetic diversity found in the Brazilian feeding grounds (Jordao et al., 2015; Jordão et al., 2015). On comparing the tracks of these two turtles with the oceanic circulation, we note an active swimming behaviour towards specific destinations; the individuals swam against the north-westward flowing Guiana current (Baklouti et al., 2007).

Conversely, turtle #149696 used prevailing currents (during the second part of the migration) to reach her destination. This individual left the French Guianan coast to perform the first transatlantic migration ever recorded in juvenile green turtles, swimming through the

Equatorial Counter-Current (Fig. 2) (Fonseca et al., 2004) and towards Guinea-Bissau and then Ghana. Guinea-Bissau is the most important nesting site for green turtles along the African coast (Catry et al., 2002), and is also a major contributor to the genetic diversity of the West Atlantic foraging grounds (Jordão et al., 2015). The probability that this turtle ended its journey either in the rookery of Guinea-Bissau or Cape Verde is reinforced by the simulations performed by Putman et al. (2013), who demonstrated that the dispersal east of 14°W accounted for 5-65% of the simulated turtles found in the Caribbean and North American foraging grounds after 5 years of simulations (Putman and Naro-Maciel, 2013). To confirm possible connections between the developmental habitat of Martinique and adult foraging/reproduction habitat, it will be necessary to equip additional immature green turtles in Martinique with longer-lasting tags such as SPOT tags, which record only the locations of animals.

The multidirectional migrations performed by these seven individuals is in accordance with the genetically mixed stock of green turtles inhabiting common developmental habitats but originating from diverse natal beaches dispersed across the Caribbean (Bass and Witzell, 2000; Jordão et al., 2015; Luke et al., 2003). Using the same genetic analyses as those already carried out for loggerhead (Engstrom et al., 2002), hawksbill (Meylan, 1999), and green turtles (Bass et al., 2006; Luke et al., 2003), we will be able to find the natal origins of these immature turtles and confirm whether they are heading for adult habitats or rather exploring new developmental habitat until they reach sexual maturity. Given that this research program aims to ensure a long-term follow up via capture and tagging (PIT) of individuals across all Martinique sites, the recapture of tagged turtles in the multiple nesting sites spread across the Atlantic will soon make it possible to link the developmental habitat of Martinique to natal rookeries. As the identification of key areas used by immature green turtles is crucial to renew future breeders, this confirms the need to track more individuals in the different Caribbean islands to ensure the conservation of this endangered species at multiple scales and stages, i.e. developmental habitat, foraging areas and reproduction habitat. Data from these studies will consolidate decision making for the application of urgent conservation measures in this extensive area composed of multiple jurisdictional waters. This study, together with newly acquired genetic data (Jordao et al. 2015), also provides up-to-date and useful tracking data that could help to improve the design and geographic limits of Regional Management Units (Wallace et al., 2010).

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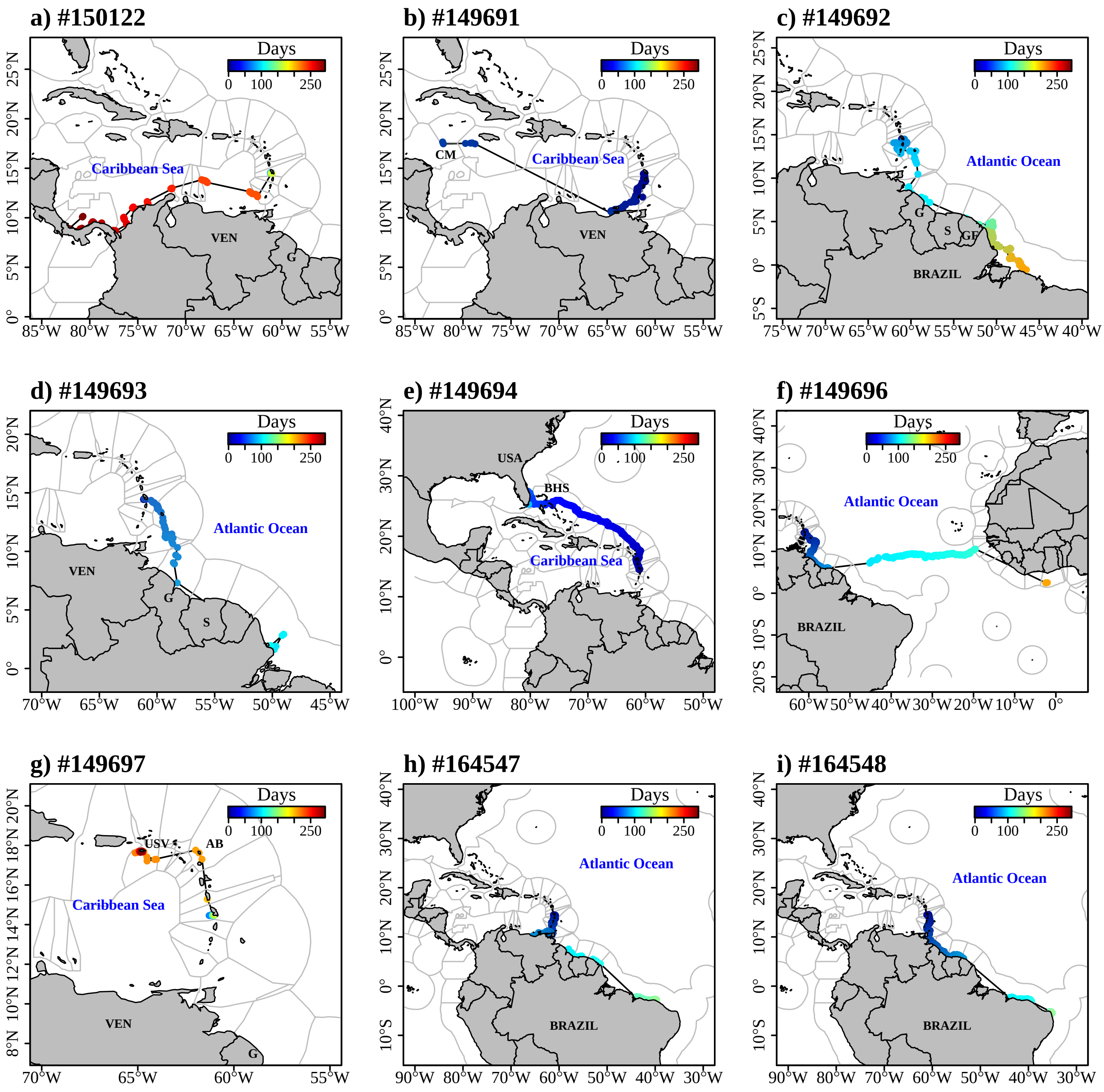
Figures captions

Fig. 1 Tracks (black lines) and locations (in colour) of the nine immature green turtles that performed developmental migration from Martinique. The colour bar indicates the time elapsed (in days) since tag deployment. The black lines with no dots refer to missing locations due to transmission issues. The grey contours refer to the Exclusive Economic Zones crossed during migration, namely AB (Antigua and Barbuda), BHS (The Bahamas), CM (the Cayman Islands), GB (Guinea-Bissau), G (Guyana), GN (Ghana), VEN (Venezuela), S (Suriname), USA (United States), USV (United States Virgin Islands).

Fig. 2 Tracks of the nine imature juveniles in relation to known home ranges of adult green turtles across the Caribbean-Atlantic region, i.e. nesting sites (in orange) and foraging grounds (in green). The white contours refer to the Exclusive Economic Zones: AB (Antigua and Barbuda), BHS (The Bahamas), COL (Colombia), CM (the Cayman Islands), CR (Costa Rica), CV (Cape Verde), GB (Guinea-Bissau), G (Guyana), GN (Ghana), MEX (Mexico), PAN (Panama), PR (Puerto Rico), VEN (Venezuela), S (Suriname), USA (United States), USV (United States Virgin Islands). The bathymetry was extracted from GEBCO (30-arc-second 1 km grid).

Table 1. Summary of the horizontal movements of the nine juvenile green turtles tracked from Martinique. PTT refers to the Platform Terminal Transmitter, Nloc to the number of locations analysed in the study, and CCL to the Curved carapace length. The numbers in italics are the mean+SD.

Ptt	**Start Date**	**End Date**	**Nloc**	**Duration (d)**	**Distance (km)**	**Speed (km.h-1)**	**Weight (kg)**	**CCL (cm)**
150122	14/10/2015	31/07/2016	225	291	3202	2.0±2.3	66.4	82
149691	03/06/2015	24/07/2015	163	51	3014	2.4±2.4	67.4	81
149692	03/06/2015	04/12/2015	289	184	4703	2.1±2.3	80.4	86
149693	02/06/2015	14/10/2015	185	134	2838	1.5±2.0	71.5	83
149694	01/06/2015	18/08/2015	445	78	3895	3.0±2.4	75.4	84
149696	03/06/2015	20/12/2015	486	200	8771	2.8±1.9	81.4	88
149697	02/06/2015	16/03/2016	580	288	1324	0.81±1.4	61.6	78.5
164547	27/10/2016	21/03/2017	553	145	5941	2,7±2,1	73.8	88
164548	25/10/2016	22/03/2017	618	148	5873	2,5±2,1	77.6	88.5
			393±179	*168±82.6*	*4395±2215*	*2.5±0.7*	*72.8±6.7*	*84.3±3.5*


a) #150122
Days
0 100 250
Caribbean Sea
VEN
G
b) #149691
Days
0 100 250
CM
Caribbean Sea
VEN
c) #149692
Days
0 100 250
Atlantic Ocean
G
S
GF
BRAZIL
d) #149693
Days
0 100 250
Atlantic Ocean
VEN
G
S
e) #149694
Days
0 100 250
USA
BHS
Caribbean Sea
f) #149696
Days
0 100 250
Atlantic Ocean
BRAZIL
g) #149697
Days
0 100 250
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AB
Caribbean Sea
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h) #164547
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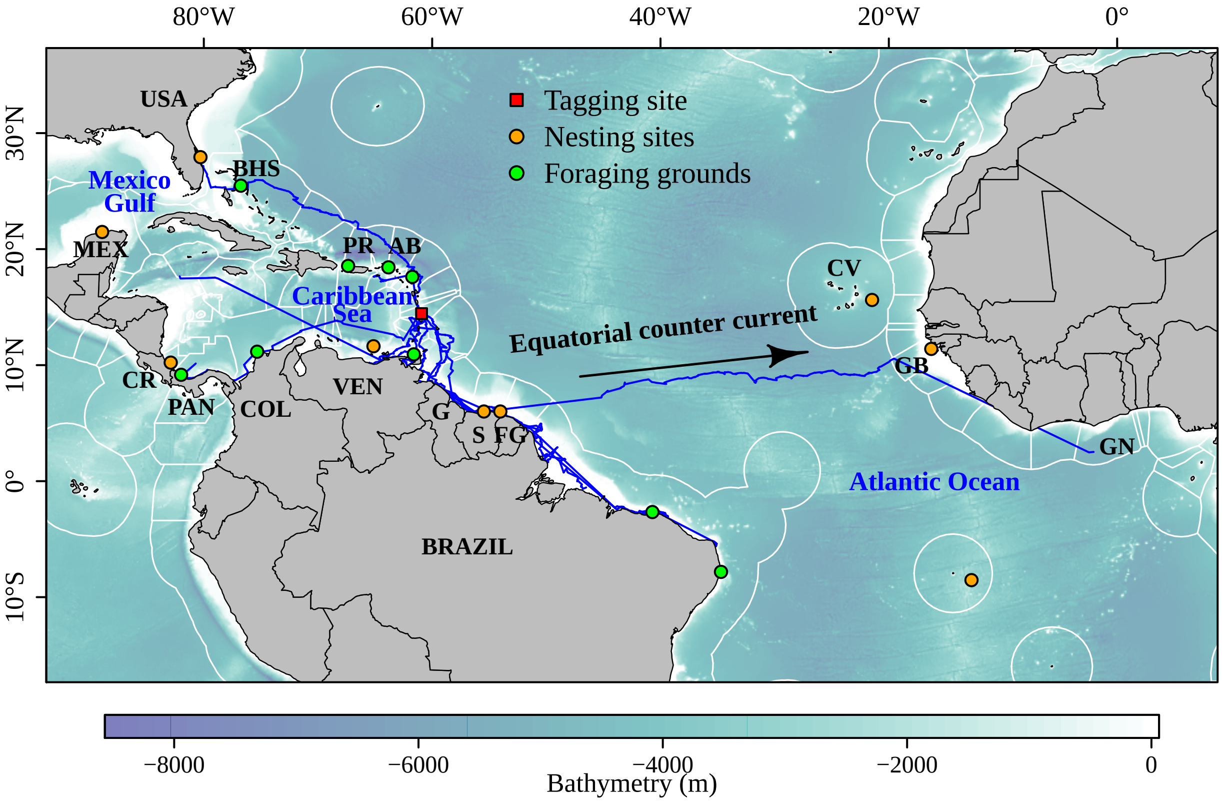
80°W
60°W
40°W
20°W
0°
30°N
20°N
10°N
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10°S
🟥 Tagging site
● Nesting sites
● Foraging grounds
USA
Mexico Gulf
BHS
MEX
PR
AB
Caribbean Sea
CR
PAN
COL
VEN
G
S
FG
BRAZIL
CV
Equatorial counter current
GB
GN
Atlantic Ocean
−8000
−6000
−4000
−2000
0
Bathymetry (m)

ANNEXE I

Residency and migratory patterns of juvenile and adult hawksbill turtles across the Caribbean

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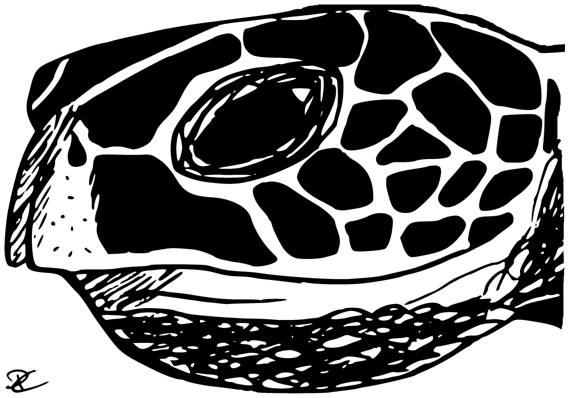
M. Nivière, **P. Chambault**, É. Dumont-Dayot, Y. Le Maho, D. Chevallier. Residency and migratory patterns of juvenile and adult hawksbill turtles across the Caribbean. *En préparation*.



Residency and migratory patterns of juvenile and adult hawksbill turtles across the Caribbean

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ABSTRACT

Incorporate animal movement into management strategies is a common challenge in species conservation, especially when dealing with a poorly studied and critically endangered species such as the hawksbill turtle *Eretmochelys imbricata*. To reach the objective of the national action plan established in 2008 in Martinique Island (French West Indies), we tracked 16 hawksbill turtles at two different life stages, i.e. juvenile and adult, and during three main activities, i.e. foraging, nesting and migrating. This study aimed to (1) investigate the site fidelity of hawksbill turtles at their habitats (developmental, inter-nesting and foraging habitats), (2) identify the migratory routes and foraging grounds used across the Caribbean and (3) assess the diving patterns of this species among the different stages. Sixteen hawksbill turtles (11 females, 3 juveniles and 2 males) were for the first time satellite tracked from Martinique Island between 2013 and 2017. Regardless the sex or the age, our results show a strong site fidelity of the individuals to the inter-nesting (females' home range: 131.7 km²), foraging grounds (males' home range: 81.2 km²) and developmental habitat (juveniles' home range: 157.3 km²). The juveniles shared 10% of their developmental habitat with the males, highlighting a critical foraging habitat which needs to be protected in Martinique. The migratory routes of the adult females revealed regional connectivity between Caribbean Islands, and the use of distinct foraging grounds. The analysis of the migration paths in relation to the intensity of fisheries activity would enable to highlight the risk areas, which is required for the implementation of adequate measures to reduce by-catch in this region. The crossing of 17 exclusive economic zones and international waters by the adult females also reinforces the need to identify key areas to ensure the conservation of this critically endangered species across the Caribbean region.

Keywords:

Eretmochelys imbricata; critically endangered; migration routes; diving behaviour; developmental habitat; foraging grounds; satellite tracking

INTRODUCTION

Incorporate animal movement into management strategies is a common challenge in species conservation. The field of movement ecology describes the animal movement by its attributes: the type of movement, i.e. nomadism, migration and residency, and the characteristics of the movement, i.e. migration distance, size and shape of the home range and stopovers (Singh et al., 2016). The recent growth of this field has highlighted numbers of challenges in wildlife management. Indeed, the protection of marine migratory species such as marine mammals, seabirds and sea turtles is difficult because of their wide distribution at-sea. Among sea turtles, the hawksbill turtle is widely distributed throughout hundred tropical and sub-tropical waters (Moncada et al., 2012). This species is also highly threatened as an unsustainable exploitation for its shell and eggs have contributed substantially to its strong population decline worldwide. The majority of this trade has ceased after the hawksbill turtle has been listed on the Annex 1 of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). However, such practice is still legal in many countries and hawksbill turtles are continuously exposed to by catch and/or destruction of their habitats both at-sea and on land. The strong population decline of hawksbill turtles (80%) has led to list this species as critically endangered on the International Union for Conservation of Nature Red List (IUCN) in 1996 (Meylan, 1999). While this species is of important conservation concern, knowledge of its behavior and distribution at-sea is still poorly understood although essential for its conservation (Hamann et al., 2010).

Delineating the high-use areas, spatially and temporally is therefore crucial for the protection of this highly mobile marine species. Over recent years, the rise of satellite telemetry has facilitated the identification of resident areas where individuals adopt an aggregative behavior which makes them particularly vulnerable (Rees et al., 2016; Shillinger et al., 2010). Although the study of hawksbill juveniles' behavior at their foraging grounds is constrained by their limited size, a few studies have shown a strong fidelity for particular areas located along Belize and British Virgin Islands, in the eastern Caribbean Sea (Scales et al., 2011; Witt et al., 2010). Furthermore, the tracking of hawksbill turtles from Mona Islands (Puerto Rico) has suggested an overlap between foraging areas used by mature males and developmental habitats used by juveniles (Diez and Dam, 2002). Complementary, the tracking of adult females has highlighted a site fidelity to their foraging grounds (Hawkes et al., 2012), where they display a strong residency pattern during two to three years before migrating back to their inter-nesting habitats (Horrocks et al., 2001). Pathways undertaken by hawksbill turtles to connect their habitats have therefore been identified in some places, and have provided crucial information on the migration behavior of this endangered species (Cuevas et al., 2008; Hawkes et al., 2012; Hoenner et al., 2012). Among research priorities highlighted to date, the importance of understanding the complex relationships among the various nesting sites and foraging areas seems crucial to apprehend population-level impacts of anthropogenic threats (Hamann et al., 2010).

In addition to surface movements, some satellite transmitters can also reveal the diving behavior of such mobile species. Depending on the purpose of the dive, i.e mating, foraging, resting or migrating, hawksbill turtles can exhibit different dive patterns, which can be described by their depths and durations (Blanco et al., 2013; Gaos et al., 2012a). The amount of activity seems therefore to fluctuate among dives and influence dive duration (Okuyama et al., 2012). Dives appear to be long throughout the inter-nesting period (Storch, 2004), suggesting that hawksbill females spend more time resting. It has also been suggested that hawksbill turtles concentrate their activities in shallow waters (< 20m), regardless of the life stage (Gaos et al., 2012b). This behavior could be associated with dietary preferences of hawksbill turtles for sponges and macroalguae, which are found in highest densities in shallow waters (León and Bjorndal, 2002; Meylan, 1999). Improving our knowledge on those dive patterns will provide complementary information, aiding therefore in managing human activities in key areas, i.e. developmental, inter-nesting and foraging habitats.

Many studies have focused on the satellite tracking of the hawksbill turtle across the Caribbean region (Blumenthal et al., 2008; Meylan, 1999; van Dam and Diez, 1998). However, the knowledge on the ecology at-sea and the diving behavior of this species is still poorly understood, especially in the French West Indies (Guadeloupe and Martinique Islands). Despite these two islands have been identified as an important nesting site for hawksbill turtles (Meylan, 1999), no study has to date been conducted in such key areas. Anthropogenic pressure and alarming situation of hawksbill’s populations in the French West Indies have led to the adoption of a prefectural decree for the protection of sea turtles in 1993 in Martinique and in 1991 in Guadeloupe. More recently, a ministerial decree was passed in 2015 to counter the population decline (Chevalier, 2005). In 2008, the French Ministry for Ecology, Sustainable Development and Energy reinforced these measures by making *Eretmochelys imbricata* a priority species of the restoration plan for sea turtles of the French West Indies. This program was supported by a national action plan in Martinique that covers the 2008-2012 period (Chevalier, 2005). One of the main objectives of this plan was to study the distribution and the diving behavior of the hawksbill turtle inhabiting the Martinique waters, for both adult and juvenile individuals.

To reach the objective of this action plan, we tracked 16 hawksbill turtles at two different life stages, i.e. juvenile and adult, and during three main activities, i.e. foraging, nesting and migrating. This study aimed to (1) investigate the site fidelity of hawksbill turtles at their habitats (developmental, inter-nesting and foraging habitats), (2) identify the migratory routes and foraging grounds used across the Caribbean and (3) assess the diving patterns of this species among the different stages. Understanding the core use areas and movements of hawksbill turtles will support the sea turtles Action Plan of the French West Indies in developing efficient conservation measures across the Caribbean region, where the populations of this critically endangered species are still threatened and declining (Meylan, 1999).

2. MATERIALS AND METHODS

2.1 Ethics statements. This study meets the legal requirements of the countries in which the work was carried out, and follows all institutional guidelines. The protocol was approved by the "Conseil National de la Protection de la Nature" (CNPN, http://www.conservation-nature.fr/acteurs2.php?id=11), and the French Ministry for Ecology, Sustainable Development and Energy (permit Number: 2013154-0037), which acts as an ethics committee in Martinique. After the evaluation of the project by the CNPN, fieldwork was carried out in strict accordance with the recommendations of the Police Prefecture of Martinique, in order to minimize the disturbance of animals.

2.2 Capture and tag deployment

Seventeen hawksbill turtles were tagged in 2013, 2015 and 2016, in three different sites in Martinique Island, in the French West Indies (Fig. 1).

2.2.1 Juveniles and males

From 09/23/2013 to 09/28/2013, three juvenile green turtles (#130775, #131353, #130778) and two male green turtles (#130772, #130777) were captured northern Martinique (Prêcheur, Diamant and Saint Luce sites, 14°79 N, -61°22 W) – see Fig. 1, site 1. Captures were conducted at a depth between 2 and 15 m. The capture of each turtle was performed by two or three freedivers, preferably when the turtle was static, i.e. resting or feeding at the bottom. When the animal was resting or feeding (head down), the freediver dived silently close to the head of the turtle, and once arrived to animal plumb, the nuchal shell and plaques of pygales shell were maintained. Once the turtle was captured, the freediving positioned the turtle against his chest, keeping her anterior flippers against his breastplate and then rose to the surface. A second diver held the foreflippers and helped to lift the individual into the boat for measurements and tagging. The turtles were equipped with Argos-Fastloc GPS tags (10-F-296B, Wildlife Computers Redmond, WA, USA). Each turtle was placed in a pen, and standard morphometric data were recorded, i.e. curved carapace length (CCL) and curved carapace width (CCW). Each individual was also marked by inserting a Passive Integrated Transponder (PIT) in the right triceps.

2.2.2 Adult females

In August 2015, southern Martinique, on Diamant (14°47 N, -61.03 W) and Sainte-Luce beaches (14°47 N, -60°96 W), six adult females were equipped with satellite tags while laying their eggs (Fig. 1, site 2). Two adult females were also equipped in August 2016 northern Martinique (Prêcheur site), and four other southern Martinique (Diamant and Saint Luce beaches). Eleven females (#150117, #150118, #150119, #150120, #150121, #162264, #162265, #162266, #162267, #162268, #162269) were fitted with Argos SPOT tag (293A, Wildlife Computers Redmond, WA, USA), and one female (#150123) with an Argos-Fastloc GPS tag (10-F-296A; Wildlife Computers Redmond, WA, USA).

2.3 Data collected from the tags. In order to provide optimum location accuracy and increase the number of positions available to counterbalance errors caused by the proximity to the shore, the Argos-Fastloc GPS tags were programmed to simultaneously record Argos and GPS locations (Costa et al., 2010; Rutz and Hays, 2009). The GPS sampling interval was set to 4-hours and the GPS locations associated with an accuracy < 100 m. Different classes of signal accuracy were provides by the Argos system: locations classes (LC) 3, 2, 1 and 0, with estimated accuracies ranging from 150 m to 2.5 km, LC A and B with no estimated accuracy, whereas LC Z indicated invalid location.

The tags provided diving data binned as 4-hours period histograms, i.e. maximum dive depth, maximum dive duration, *in situ* temperature and proportion of time spent at each temperature (TAT in %). In 2013, maximum dive depths were collected every 10 m from 10 to 100 m, and then every 50 m from 100 to 250 m. Maximum dive durations were stored from 30 s to 1 min, then every minute from 1 to 5 min, every 5 minutes from 5 to 10 min, and finally every 10 minutes from 10 to 60 min. *In situ* temperatures were recorded during dives from 20 to 32 °C, every one degree Celsius.

Argos FastLoc 296A deployed in 2015 (#150123) was configured to collect maximum depths every 5 m from 0 to 20 m, then every 10 m from 20 to 100 m and then every 50 m from 100 to 250 m. Maximum dive durations were stored every minute from 1 to 5 min, every 5 minutes from 5 to 30 min, and finally every 10 minutes from 30 to 60 min. *In situ* temperatures were recorded from 0 to 33 °C, every one degree Celsius.

Argos SPOT 293A tags deployed in 2015 were programmed to provide only the locations of turtles by recording Argos locations, those deployed in 2016 were programmed to record *in situ* temperatures every 5 °C from 10 to 20 °C, every 2 °C from 20 to 30 °C, and finally for 33 °C and 60 °C.

2.4 Data pre-filtering. Data were downloaded daily via Argos Message Retriever (WC-DAP, Wildlife Computers-Data Analysis Programs). Argos position estimates were enhanced by applying of Kalman-filtering algorithm to account for Argos errors (CLS, Collecte Localisation Satellites, Toulouse, France). The strong proximity to the shore and the possible Argos error resulted in 40% of the positions being found on land after applying the Kalman filter in 2013, and 12.7% in 2015 and 2016. The altimetry product provided by the Hydrographic and Oceanographic Service of the French Navy (SHOM) at a 25 m² resolution was used to identify these erroneous locations and discard them. The locations of class Z, considered insufficiently accurate, and those associated with a travel speed of over > 5 km.h^{-1} were also discarded (1.8% in 2013 and 18% in 2015 and 2016) (Schofield et al., 2013). Data collected by the tag of the individual #150119 were not analyzed because this turtle has been unfitted when she was caught in the mangrove. Thus, a total of sixteen turtles have been analyzed in this study.

2.5 Spatial analysis. All analyses were carried out using R software version 3.3.3 (R Core Team, 2016). Distance traveled between two successive locations and the net distance traveled, calculated in straight-line between the first and the last locations for each turtle, were calculated using the *trackDistance* function from the *trip* package (Sumner, 2016). The speed was then derived from the calculated distance and time elapsed between paired locations. The date of migration departure has been determined for each adult female tracked in 2015 and 2016 by performing a spatial query (Baudouin et al., 2015; Chambault et al., 2015; Chambault et al., 2016a). To identify potential foraging grounds, post-nesting migration routes of the 12 females were analyzed by measuring the proportion of the time spent in each cell grid (resolution of 33.4 x 33.4 km), and calculated using the *tripGrid* function from the *trip* package (Sumner, 2016). Areas where a female remained at least three days was considered as a stopover (Baudouin et al., 2015). Data sets of the females were split into three groups according to the stage, namely the inter-nesting, migration and potential foraging grounds.

2.6 Kernel analysis. In order to display the residency patterns of the juveniles, the males and the females (during the inter-nesting season and at the foraging grounds), home ranges were estimated using the kernel density distributions (KDE) based on both the Argos and GPS positions (Worton, 1989). To minimize the autocorrelation in spatial analysis, for each turtle, the median daily locations were calculated (Schofield et al., 2013). For the home range calculation, a minimum of five median daily locations has been required. Using the *kernelUD* function from the *adehabitatHR* package (Calenge, 2006), kernel densities were estimated for the juveniles (*n*=3), the males (*n*=2) and the gravid females at both their inter-nesting (*n*=9) and potential foraging habitats (*n*=8). The minimum smoothing parameter was used (Gitzen et al., 2006; Worton, 1989), and the 50% kernel contour to identify the core use area and the 95% contour for the broad home range. The overlap between juveniles’ home range and males’ home range was measured by extracting the kernel contours using the function *getverticesHR* from the *adehabitatHR* package (Calenge, 2006). Then the intersection between extracted contours was estimated using the function *gIntersection* from the *rgeos* package (Bivand and Rundel, 2017).

2.7 Dive analysis. The dive data for the females were split into three groups according to the habitat, namely the inter-nesting habitat, migration and potential foraging grounds. To enable a comparison of the diving behavior among the resident turtles, the dive data of the female collected during the inter-nesting period (*n*=9) were analyzed together with those of the juveniles (*n*=3) and the males (*n*=2).

2.8 Statistical analysis. All statistical analyses were carried out using R software version 3.3.3 (R Core Team, 2017). Normality and homogeneity of variances were checked using Shapiro-Wilcoxon test. Non-parametric tests, either Kruskal-Wallis or Wilcoxon was used to compare dive behavior between juveniles, males and females and also between individuals within each group. Values are shown as means±SD.

3. RESULTS

3.1 Sedentary movements. The three juvenile hawksbill turtles (#130775, #130778 and #131353) measured on average 51.5±4.8 cm in length (CCL range: 48-57 cm; #131353 vs. #130775), and on average 45.3±6.2 cm in width (CCW range: 41.5-52.5 cm, #131353 vs. #130778) - see Table 1. These individuals were tracked during 208±50 d (range: 162-288 d, #130778 vs. #131353). The three turtles traveled from 944 (#130775) to 1081 km (#131353, mean±SD: 965.7±106.2 km). The tracked individuals traveled at an average speed of 0.3±0.1 $km.h^{-1}$. All the juveniles occupied a mean home range (KDE) covering 157.3±71.2 km² (range: 77.0-212.8 km², #131353: 140 locations vs. #130778: 166 locations), and a core area of 12.1±4.2 km² (range: 7.4-15.2 km², #131353 vs. #130778), located northern of Martinique, close to the capture site (Table 2 and Fig. 2a).

The two males were tracked during 148 and 359 d, respectively (#130772 vs. #130777) - see Table 1. Their mean CCL was 80.4±7.6 cm, and they measured 70±2.9 cm in width. They traveled an average of 1089±718.4 km, at an average speed of 0.3±0.01 $km.h^{-1}$. These two males established a home range close to release site, located northern of Martinique. Both males occupied a home range (KDE) of 81.2±35.9 km² (#130772: 55.8 km² and 106 locations; #130777: 106.6 km² and 269 locations), with a core area covering 9.1±3.7 km² (#130772: 6.5 and #130777: 11.8 km²) – see Table 2 and Fig. 2b.

Given that the migration departure of two females (#150117 and #150118) occurred right after tag deployment, only nine females (over the 11 equipped) were considered for the analysis during the inter-nesting period. The individuals were tracked during 1 to 27 d (#150123 vs. #150121 and #162265, mean: 14.5 ± 8.9) and traveled 3 to 251 km (#150123 vs. #150121, mean: 65.7±79.9 km), at an average speed of 0.2±0.1 km.h^{-1} (Table 1). As the number of locations recorded during the inter-nesting season was low, the kernel density could not be estimated for the individuals #150123 *(n=3)*, #162266 *(n=3)* and #162267 *(n=2)*. The six remaining females occupied a home range (KDE) of 131.7±137.7 km², located southern of Martinique, with a core area of 34.2±33.9 km² (Table 2 and Fig. 2c).

3.2 Migration movements. The post-nesting movements of the eleven females equipped in 2015 and 2016 were recorded during 5 to 93 d (#150117 vs. #162269). Three migratory patterns were observed as three individuals (#150117, #150123 and #162266) migrated westward, reaching the Nicaraguan coast, whereas the four other females (#150118, #150120, #162264 and #162268) migrated southward, reaching the Grenada and Grenadines islands, and the last two females (#162267 and #162269) migrated northward, reaching the Bahamas and the Turks and Caicos Islands (Fig. 3). The group of adult females traveled through the international waters of 31 exclusive economic zones (EEZ). The individuals #150117, #150123 and #162266 traveled on average 2224±581 km, for a net distance of 2313±134 km (Table 2). Their averaged speed was 1.80±0.54 km.h^{-1}. The individuals #162267 and #162269 traveled on average 2326±715 km, over a net distance of 1630±367 km. Their average speed was 2.30±0.71 km.h^{-1}. These individuals traveled on average 309±98 km, over a net distance of 191±51 km, at an average speed of 1.71±0.14 km.h^{-1}. Along these migratory pathways, four stopovers were highlighted (Figs. 3a and b). No stopover was identified for the turtles migrating southward, whereas the maximum number of stopovers obtained for one turtle is two (#162266).

3.3 Potential foraging grounds. Based on the analysis of the time spent per cell grid, eight potentials foraging grounds were identified. The tag #150121, #162265 and #162267 ceased emitting after recording too few locations, preventing from identifying any foraging area. Three potential foraging grounds were identified off Nicaragua, as the turtle #150117 reached the biological reserve of Cayos Misquitos (14°32 N, 82°41 W), where she remained during 70 d (Fig.

3a). The turtles #150123 and #162266 remained 100 and 108 d within the Bawihka Channel (15°47 N, 81°41 W) – see Fig. 3b. These two females occupied a foraging area (95% kernel contour) of 206 and 162 km², respectively, with a core use area (50%) covering 26 and 23 km², respectively. The female #150117 occupied a home range area of 731 km², with a core use area covering 123 km² (Table 3).

Four other potential foraging areas were located further south of Martinique. The first, located in Northern of Grenada Island (12°13 N, 61°35 W) was occupied by individuals #150120 during 63 d. The second was located near Carriacou Island, where the individual #150118 remained for 118 d (12°29 N, 61°23 W) – see Fig. 3c. At this latter foraging ground, this turtle occupied a home range area of 802 km², with a core area covering 136 km², whereas the turtle #150120 occupied a home range of 187 km² with a core use area covering 43 km² (Table 3).

Among the turtles fitted in 2016, the individuals #162264 and #162268 remained 145 and 125 d near St Vincent and the Grenadines Islands (Fig. 3c). They occupied a home range of 101 and 314 km², with a core use area of 13 and 43 km² (Table 3). Another female (#162269) fitted in 2016 occupied a home range of 43 km² with a core use area of 7 km², located near Bahamas Island (24°04 N, -77°19 W) – see Fig. 2b. This turtle remained in this place for 68 d.

3.4 Diving behavior. The three juveniles performed mainly shallow (15.6±9.6 m) and long dives (49±17 min) – see Figs. 4a and b. The *in situ* temperatures recorded ranged from 27 to 33 °C (mean: 28.9±1.3 °C) – see Fig. 4c. Despite the inter-individual variability regarding the maximum depth ($p < 0.001$, $X^2=243$) and the dive duration ($p < 0.001$, Kruskal-Wallis test, $X^2=124$), the majority of the dives were shallow (63% between 0-10m) and long (25% between 60-70 min).

The males ($n=2$) dived on average at 15.6±5.7 m during 53.0±20.3 min (Figs. 4d and e). The dives were shallow (97% at 0-20 m) and long (50% between 60 and 70 min), and the average temperature recorded was 29.0±1.2 °C (range: 27-32 °C) – see Fig. 4f. Similarly to the juveniles, there was an inter-individual variability between the two males regarding the depth ($p < 0.001$, Kruskal-Wallis test, $X^2=28$) and the duration ($p < 0.001$, Kruskal-Wallis test, $X^2= 18$).

During the inter-nesting season, the turtle #150123 dived on average at 31.1±19.4 m (50% between 0-20 m) during an average duration of 19.6±18.6 min (57% lasted 0-10 min) – see Figs. 4g and h. During migration, the female #150123 spent 48% of the dives between 0-20 m and 37% between 40-60 m (mean: 30.2±22.2 m) – see Fig 4g. The average duration of those dives were

24.0±18.7 min (31% lasted 0-5 min and 24% lasted 35-40 min) – see Figs. 4g and h. At the foraging ground, this turtle performed all deeper dives between 20-60 m (mean: 41.7±9.4 m) and long dives (94% between 35-50 min, mean: 42.9±8.9 min) – see Figs. 4g and h. Dive depth and dive duration differed significantly between the three phases ($p < 0.001$, Kruskal-Wallis test, $X^2=26$; $p < 0.001$ vs. $X^2=47$, respectively).

The *in situ* temperatures recorded for the eight adult females (#150118, #150121, #150123, #162264, #162265, #162266, #162268 and #162269) during the inter-nesting season varied from 28 to 33 °C, and were on average 29.2±0.7 °C (Fig. 4i). During migration the *in situ* temperatures recorded were an average of 29.6±1.4 °C (range: 26 to 33 °C) whereas they were an average of 28.7±1.0 (range: 24 to 33 °C) at the foraging ground. The average *in situ* temperature differed significantly during these three phases ($p < 0.001$, Kruskal-Wallis test, $X^2=5440$).

By selecting the inter-nesting period for the females, the dive duration was significantly different between adults and juveniles ($p < 0.001$, Kruskal-Wallis test, $X^2=344$; $p < 0.001$), whereas the dive depth did not differ between the two stages (Wilcoxon test, W=7; $p = 0.4$). Among the adults, the dive duration and the dive depth differed significantly according to the individual ($p < 0.001$, Kruskal-Wallis test, $X^2=105$; $p < 0.001$, W=76, respectively).

4. DISCUSSION

This study is the first to describe both the horizontal and vertical movements of hawksbill turtles in Martinique at different stages (juvenile and adult) and for both sexes.

4.1 Residential key areas

The three juveniles tracked in 2013 established home ranges in the north of Martinique covering between 77 and 212 km² (mean±SD: 157±71 km²). Comparison with other home range estimates for hawksbill juveniles tagged elsewhere is limited due to the low number of previous tracking of this species. However, the few studies that estimated the home ranges of juvenile hawksbill were reported to cover an area of ≤ 1 km² (Cuevas et al., 2008; van Dam and Diez, 1998). Our estimation of the home range size was substantially larger than most previously reported, probably due to the difference in the tracking duration (11-16 d and 24 h vs. 188 d in our study), sample size (87 and

10 turtles vs. 3 in our study) or the smoothing parameter. Indeed, the KDE method is very sensitive to the smoothing parameter and could under or over-estimates the home range size (Gitzen et al., 2006; Worton, 1989). A temporary exploration out of the home range could explain such differences. Estimations of the home range size by KDE and MCP methods could also be influenced by the proximity to the shore, which led to a large number of erroneous locations on land. Nonetheless, our study enabled to observe that juveniles shared 41% of their developmental habitat with the tracked males. These latter also established an average home range of 81±36 km² located in the north of Martinique. The males remained in this area during 148 d (#130772) and 359 d (#130777), which tends to confirm the strong fidelity to this foraging area and a residency pattern for these individuals. Previous studies have highlighted similar patterns of sharing habitats between different life stages for different species such as green turtles and loggerhead turtles (Meylan, 2011). Indeed, hawksbill juveniles and males were observed on the same area in Puerto Rico (Diez and Dam, 2002).

The six females tracked in 2015 and 2016 have also established a home range close to the tagging site, in the south and north of Martinique (home range size: 135±154 km² estimated with KDE method). The very low number of locations recorded for the females during their inter-nesting period led to a bias in the estimation of the home range size. Despite the risk of damage on the tags due to resting between the cracks of the rocks or mating behavior (Godley et al., 2007), additional gravid females should be equipped earlier in the season to increase the sample size and therefore improve the home range estimation.

4.2 Migratory routes and foraging hotspots

Although both juvenile and adult hawksbill turtles have shown a strong fidelity to their foraging and inter-nesting habitats, some of them also performed a migration. A trichotomy in the migratory behavior have been observed as three adult females (#150117, #150123 and #162266) performed a long migration (mean±SD: 2924±581 km), heading westwards towards the Nicaraguan coast, the four other females (#150118, #150120, #162268 and #162264) performed a shorter migration (mean±SD: 309±98 km), heading southward and reaching Sainte-Lucia and Grenada Islands, whereas the two last (#162269, #162268) performed a long migration (mean±SD: 2326±751 km), heading northward towards Bahamian Island. An influence of oceanic currents has been highlighted only for the turtles which crossed the Caribbean Sea to reach the Nicaraguan coast. These results associated with previous studies describing the movements of hawksbill turtles across the Caribbean (Horrocks et al., 2001; Moncada et al., 2012) are consistent with genetic studies showing that nesting populations in the Caribbean come from a strong genetic mixing (Bass et al., 2006; Browne et al., 2010). According to Lutz et al. (2002), hawksbill turtles exhibited similar pattern than green turtles migrating to well-established foraging areas near shore. Our study identified five potential foraging areas with two located off the coast of Nicaragua, in the biological reserve of Cayos Misquitos (14°32 N, 82°41 W) and in the Bawihka Channel (15°47 N, 81°41 W). Two others were located in the northern of Grenada Island (12°13 N, 61°35 W) and near Carriacou Island (12°29 N, 61°23 W), and two last near the Bahamas Island (24°04 N, -77°19W). The Nicaraguan coast has been described as an important foraging area for hawksbill turtles (Cuevas et al., 2008; Hawkes et al., 2012; Moncada et al., 2012), which is in agreement with our results. Although the literature on the waters of Nicaragua is very limited (Godley et al., 2007), the existence of a large coral ecosystem off the Nicaraguan and Honduran coasts seems to support the hypothesis of a feeding area for this species. Besides the foraging grounds, four areas of migratory stopovers were also identified, only for turtles migrating towards the Nicaraguan coast. Similarly to the French Guianese green turtles (Baudouin et al., 2015a), the female hawksbill turtles of Martinique remained for short periods (at least five days) in some areas during their post-nesting migration. As shown in green turtles (Baudouin et al., 2015; Philippine Chambault et al., 2016b), hawksbill could be a capital breeder, meaning that the females build up body reserves on their feeding areas and do not feed during the nesting period. Such behavior suggests that these stopovers areas could be used by these capital breeders to restore their body reserves on the way to reach their final feeding areas (Baudouin et al., 2015).

4.3 Diving behavior

In addition to the characterization of horizontal movements, the diving behavior was characterized by the depth utilization of free-living hawksbill turtles. Sea turtles have the capacity to adjust their buoyancy by controlling their lung volume. Their dive depths are therefore generally constrained within the range over which the buoyancy can be regulated (Hays et al., 2004). However, a strong variability between individuals has been observed and may indicate a niche partitioning to reduce intraspecific competition (Blumenthal et al., 2008). Similar diving patterns have been observed for both juveniles and males tracked in Martinique, as they performed mainly shallow and long dives. The mean dive depths recorded by the juveniles (15.7±9.6 m) were deeper than those recorded in Mona Islands - Puerto Rico (4.7 m, 8-10 m, van Dam and Diez, 1996; van Dam and Diez, 1998), and those recorded in the British Virgin Islands (5.1±7.4 m, Witt et al., 2010). The diving behavior could be influenced by the spatial distribution of preferred dietary items and physical conditions, e.g. wave action or predator avoidance tactics (Dam and Diez, 1996). Indeed, sponges are the preferentially diet item of hawksbill turtles (Meylan, 1999; Rincon-Diaz et al., 2011a, 2011b), and this resource is generally abundant in shallow waters (León and Bjorndal, 2002). In Martinique, the sponges distribition seems to be homogeneous throughout the coast and abundant until 15 m deep (Agence des Aires Marines Protégées and DIREN Martinique, 2010). Juveniles and males performed the majority of their dives in shallow waters (range: 0-80 m), where sponges are found in highest densities, suggesting a foraging behavior. During the inter-nesting period, the diving data recorded from the only female fitted with a time-depth-recorder have shown a majority of dives performed between 0-10 m. However, deepest dives may enable the turtles to reach zones of high sponges density, namely the “sponge belt,” at depths of 80-120 m (Ghiold et al., 1994). It has been hypothesized that the inter-nesting behavior of sea turtles is driven by the optimization of energy reserves depending on the local conditions of the habitat (Houghton et al., 2002). Various techniques such as the Inter-Mandibular Angle Sensor (IMASEN), recording the mouth opening and buccal pumping, 3D-accelerometers associated with an on-board camera and direct observation are useful to explore these hypotheses (Houghton et al., 2008; Walcott et al., 2013a). In contrast, at their potential final feeding areas, the females performed all their dives in shallow waters (20-60m). This depth utilization suggests a foraging behavior but could also be constrained by the bathymetry (Witt et al., 2010). During migration, the turtle #150123 performed exclusively shallow dives (0-20 m), likely to reduce the transit duration to reach the foraging area as fast as possible (Hays et al., 2000). It has been concluded that changes in water temperature could have an effect on the diving behavior of hawksbill turtles, influencing dive duration (Storch, 2004). In our study, all individuals occupied water temperatures between 24-34 °C, with an average of 36 °C for the female and 29 °C for the juveniles and the males. These warm temperatures physiologically constrain the turtles to come back to the surface more often (Southwood et al., 2003), but may also facilitate food digestion and built-up fat stores more rapidly (Krawchuk and Brooks, 1998).

4.4 Conclusion and conservation implications

This study highlighted critical hotspots identified both in Martinique and across the Caribbean for both sexes and different life stages. Identifying areas of high use along beaches of Martinique is important to define protected areas and implement effective management of interactions between hawksbill turtles and human activities. Moreover, information provided on the post-nesting migratory behavior of hawksbill turtles nesting on this island revealed regional connectivity between Caribbean Islands. Highlighting key elements of connectivity such as stopover sites and migratory corridors is essential for the management of this highly migrant species (Stokes et al., 2015). Likewise, the analysis of migration paths in relation to the intensity of fisheries makes an important part in the effort to reduce the risk of by-catch occurring in the open sea (Gilman et al., 2006; Hall et al., 2000). Historical inventories carried out during the last hundred years estimated the decline of hawksbill's populations worldwide to 90% (Mast et al., 2008). This estimation has been biased by the shifting baseline syndrome (Pauly and Christensen, 1995), meaning that already reduced populations are taken as references and are considered as normality. The tracked individuals traveled across 17 EEZ, reinforcing the need for the implementation of a cooperative network at the Caribbean scale, to ensure the efficient conservation of this critically endangered species.

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Figures captions

Fig 1. Study area located in the French West Indies, in Martinique Island (red rectangle). The three tagging sites are presented in the red rectangle on the up right of the figure, namely: Prêcheur (1), Diamant (2) and Saint Luce sites (3).

Fig 2. Kernel density contours (90% in turquoise and 50% in dark blue) of the adult juveniles (a, *n*=3), the males (b, *n*=2) and the adult females during the inter-nesting season (c, *n*=9).

Fig 3. Migratory routes and time spent per pixel (in days) for the 11 female hawksbill turtles during their post-nesting migration. The potential foraging grounds refer to the red cells, and the departure point to the triangle. (a) #150117, #150123, #150121 and #162266; (b) #162267 and #162269; (c) #162268, #162264, #162265, #150118 and #150120.

Fig 4. Histograms of the maximum dive depth (a, d and g), the dive duration (b, e and h) and the temperature (c, f and i) for the juveniles (a, b and c, *n*=3), the males (d, e and f, *n*=2) and the females (g, h and I, *n*=9).

Table 1. Summary of the residency movements of the juveniles (*n*=3), adult males (*n*=2) and adult females (during inter-nesting period *n*=9). *Eretmochelys imbricata*. CCL: Curved Carapace Length (cm), CCW: Curved Carapace Width.

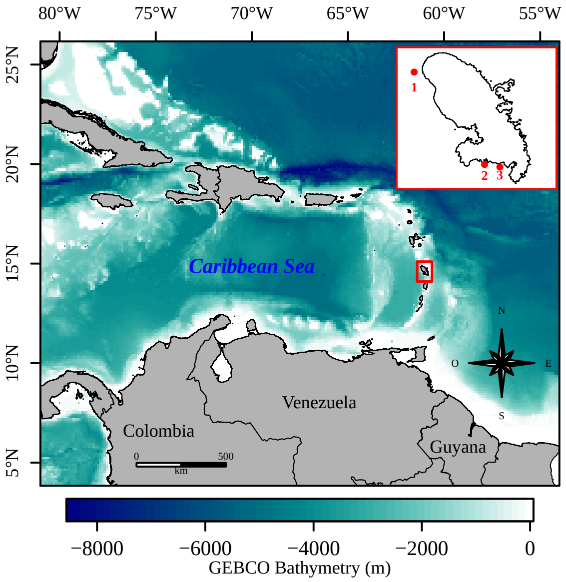
Turtle's ID	Class	Nloc	Tracking dates	Tracking duration (d)	Distance (km)	Speed ($km.h^{-1}$)	CCL (cm)	CCW (cm)	Kernel 50% (km^2)	Kernel 95% (km^2)
130775	Juvenile	133	2013/10/03 – 2014/03/25	173	944	0.37	57	42	13.9	182.2
130778	Juvenile	140	2013/09/30 -2014/03/11	162	872	0.38	49.5	52.5	7.4	77.0
131353	Juvenile	166	2013/09/26 – 2014/07/11	288	1081	0.27	48	41.5	15.2	212.8
Mean±SD		**146±17**		**208±50**	**965.7±106.2**	**0.3±0.06**	**51.5±4.8**	**45.3±6.2**	**12.2±4.2**	**157.3±71.2**
130772	Male	106	2013/09/29 – 2014/02/24	148	581	0.32	75	68	6.5	55.8
130777	Male	269	2013/11/12 – 2014/11/06	359	1597	0.3	85.8	72.1	11.8	106.6
Mean±SD		**187±115**		**253±149**	**1089±718.4**	**0.31±0.01**	**80.4 ± 7.6**	**70.0 ± 2.9**	**9.1 ± 3.7**	**81.2 ± 35.9**
150120	Female	5	2015/08/24 – 2015/09/09	16	69	0.13	-	-	39.1	102.6
150121	Female	17	2015/08/19 – 2015/09/15	27	251	0.41	-	-	104.2	419.4
150123	Female	3	2015/08/17 – 2015/08/21	4	3	0.03	-	-	-	-
162269	Female	5	2016/07/30 – 2016/08/12	13	33	0.19	-	-	34.3	178.2
162268	Female	7	2016/07/21 – 2016/08/01	11	21	0.06	-	-	5.9	22.1
162267	Female	2	2016/07/28 – 2016/07/29	1	9	0.36	-	-	-	-
162266	Female	3	2016/07/25 – 2016/08/11	17	19	0.04	-	-	-	-
162265	Female	25	2016/08/03 – 2016/08/30	27	131	0.25	-	-	12.2	38.0
162264	Female	12	2016/08/05 – 2016/08/20	15	55	0.1	-	-	9.41	29.8
Mean±SD		**9±8**		**14±9**	**65.7±79.9**	**0.2±0.1**			**34.2 ± 33.9**	**131.7 ± 137.7**

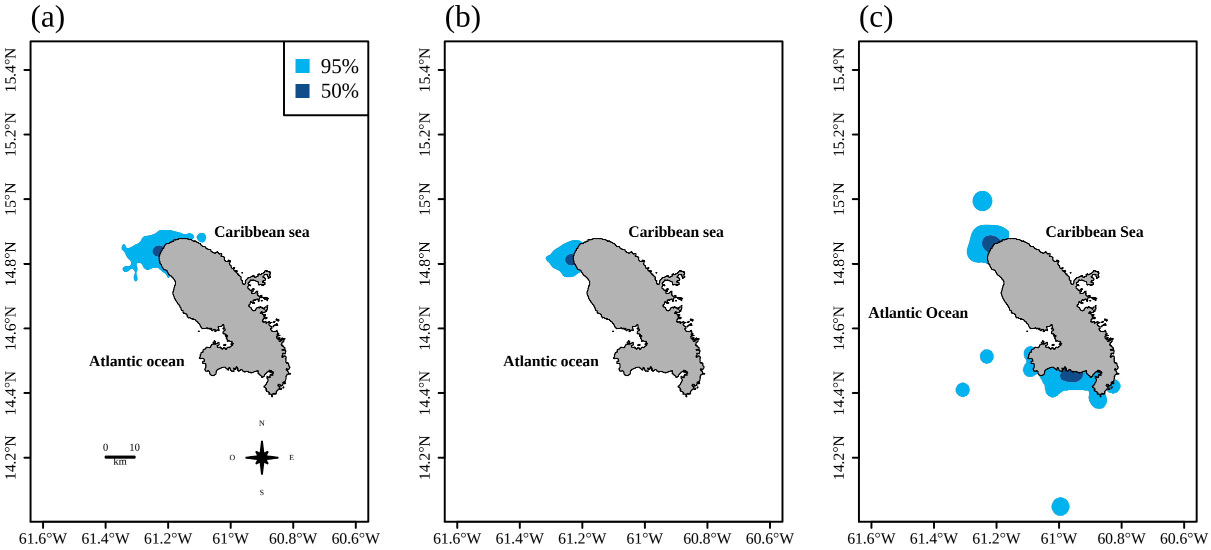
Table 2. Summary of the migration movements of the adult females during migration (*n*=11).

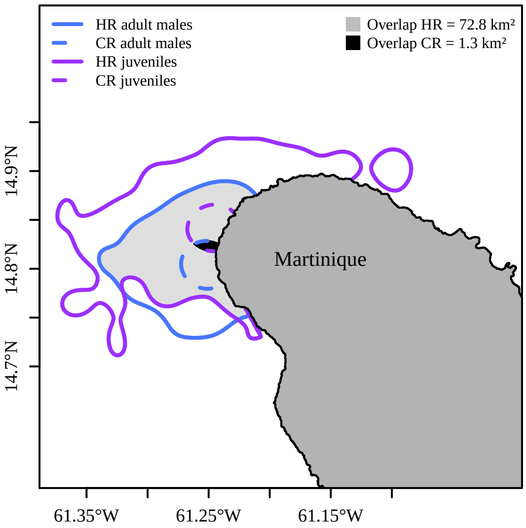
Turtle's ID	**Nloc**	**Tracking dates**	**Tracking duration (d)**	**Distance (km)**	**Speed (km.h^{-1})**	**Net straight line distance (km^2)**	**Max displacement (km)**
150121	27	15/09/15 – 15/10/23	38	1627	2.1	1381	745
162265	385	16/08/30 – 16/11/13	75	2491	1.74	433	89
150117	6	15/08/27 – 15/10/26	60	2508	2.18	2468	1708
150123	559	15/08/23 – 16/10/13	420	3587	1.18	2237	167
162266	58	16/08/13 – 16/10/06	54	2677	2.04	2234	571
Mean±SD	**208±305**		**178±210**	**2924±520**	**1.80±0.5**	**2313±134**	**815±799**
150118	23	15/08/23 – 15/08/28	5	189	1.72	121	41
150120	12	15/11/09 – 15/09/20	9	272	1.58	184	96
162268	24	16/08/14 – 16/08/27	13	373	1.64	231	70
162264	59	16/08/20 – 16/08/30	10	404	1.91	227	33
Mean±SD	**29±20**		**9±3**	**309±98**	**1.71±0.1**	**191±51**	**60±29**
162267	358	16/07/29 – 16-08/30	32	1795	2.8	1371	34
162269	605	16/08/12 – 16/11/13	93	2857	1.8	1890	42
Mean±SD	**481±175**		**62±43**	**2326±751**	**2.30±0.7**	**1630±367**	**38±6**
Mean	**192±236**		**73±118**	**1707±1221**	**1.88±0.4**	**1162±946**	**324±519**

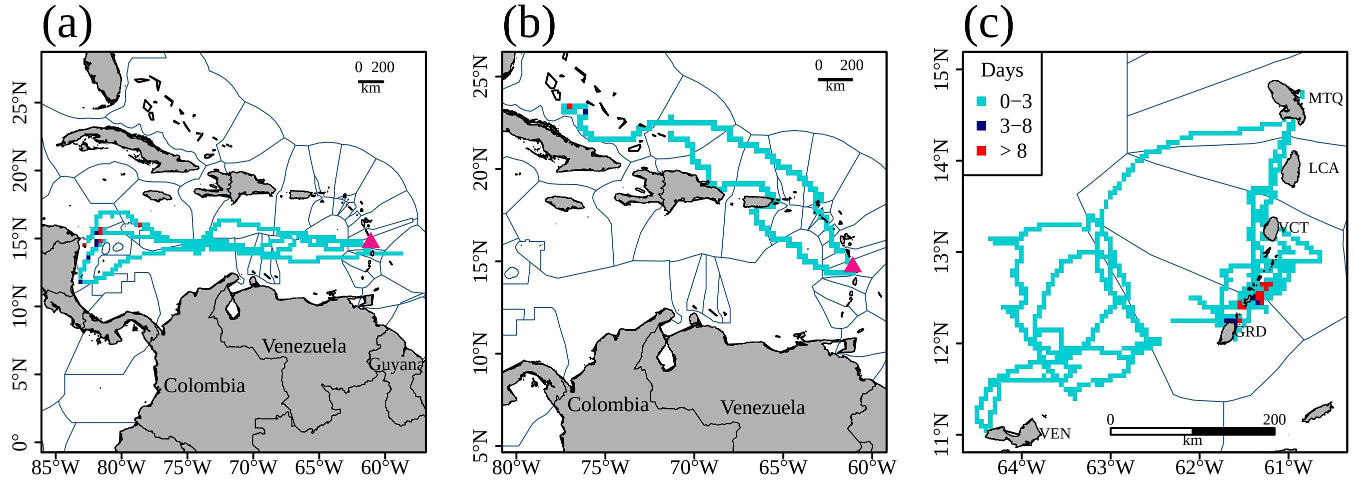
Table 3. Summary of the horizontal movements of the adult females in foraging ground (*n*=9).

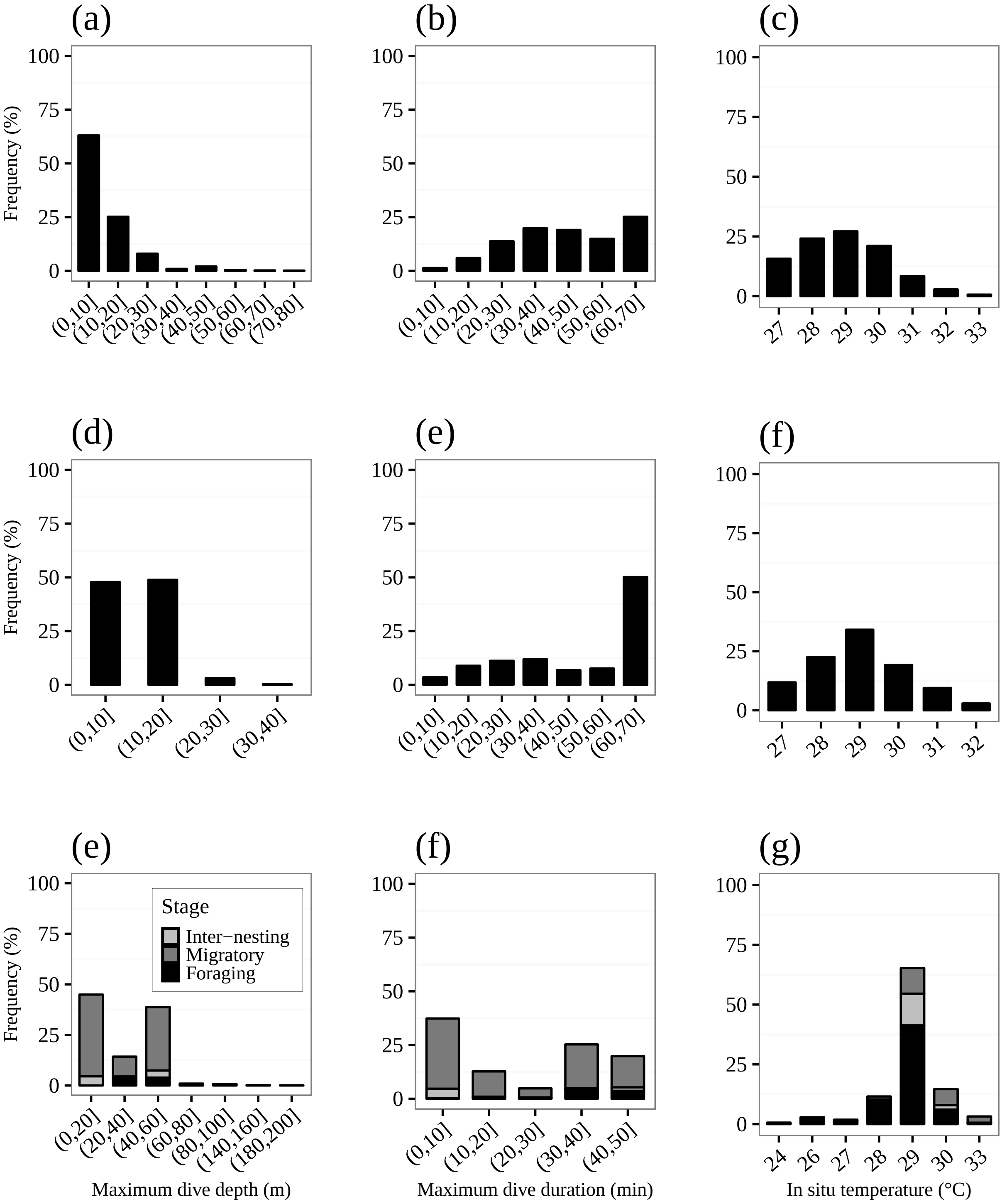
Turtle's ID	**Nloc**	**Tracking dates**	**Tracking duration (d)**	**Kernel 50% (km^2)**	**Kernel 95% (km^2)**
150117	28	2015/10/26 – 2016/01/04	70	123.2	731.6
150118	43	2015/08/28 – 2015/12/24	118	136.2	802.4
150120	20	2015/09/23 – 2015/11/25	63	43.9	187.6
150123	65	2016/10/16 – 2017/01/24	100	26.9	206.4
162269	55	2016/11/13 – 2017/01/20	68	7.2	43.5
162268	85	2016/09/03 – 2017/01/06	125	42.4	314.6
162266	97	2016/10/07 – 2017/01/23	108	23.7	162.3
162264	140	2016/08/31 – 2017/01/23	145	13.3	101.7
Mean±SD	**67±40**		**100±30**	**52.1±49.6**	**318.8±288.3**


80°W
75°W
70°W
65°W
60°W
55°W
25°N
20°N
15°N
10°N
5°N
1
2
3
Caribbean Sea
N
O
E
S
Venezuela
Colombia
Guyana
0
500
km
−8000
−6000
−4000
−2000
0
GEBCO Bathymetry (m)


(a)
(b)
(c)
95%
50%
Caribbean sea
Atlantic ocean
Caribbean Sea
Atlantic Ocean
0
10
km
N
O
E
S
15.4°N
15.2°N
15°N
14.8°N
14.6°N
14.4°N
14.2°N
61.6°W
61.4°W
61.2°W
61°W
60.8°W
60.6°W


HR adult males
CR adult males
HR juveniles
CR juveniles
Overlap HR = 72.8 km²
Overlap CR = 1.3 km²
Martinique
14.9°N
14.8°N
14.7°N
61.35°W
61.25°W
61.15°W


(a)
0 200
km
25°N
20°N
15°N
10°N
5°N
0°
85°W
80°W
75°W
70°W
65°W
60°W
Colombia
Venezuela
Guyana
(b)
0 200
km
25°N
20°N
15°N
10°N
5°N
80°W
75°W
70°W
65°W
60°W
Colombia
Venezuela
(c)
Days
0−3
3−8
> 8
15°N
14°N
13°N
12°N
11°N
64°W
63°W
62°W
61°W
MTQ
LCA
VCT
GRD
VEN
0
200
km


(a)
(b)
(c)
(d)
(e)
(f)
(e)
(f)
(g)
Frequency (%)
0
25
50
75
100
(0,10]
(10,20]
(20,30]
(30,40]
(40,50]
(50,60]
(60,70]
(70,80]
27
28
29
30
31
32
33
(0,20]
(20,40]
(40,60]
(60,80]
(80,100]
(140,160]
(180,200]
24
26
Stage
Inter−nesting
Migratory
Foraging
Maximum dive depth (m)
Maximum dive duration (min)
In situ temperature (°C)

Philippine CHAMBAULT

Distribution et comportement de plongée des tortues marines de Guyane française sous l'influence des structures océanographiques

Résumé en français

La forte hétérogénéité de l'écosystème marin se traduit par une production inégale des ressources sur un large éventail d'échelles spatio-temporelles, qui conditionne par conséquent les déplacements des tortues marines. Considéré comme l'un des plus dynamiques au monde, le plateau des Guyanes est une région très complexe d'un point de vue océanographique et qui héberge trois des sept espèces de tortues marines présentes dans le monde (la tortue olivâtre, la tortue verte et la tortue luth). L'objectif de cette thèse était de comprendre comment les contraintes océanographiques peuvent-elles influencer les déplacements en mer de ces trois espèces. Le déploiement de 55 balises satellites sur des femelles reproductrices en Guyane française a permis de fournir des informations sur leurs trajectoires, sur leur comportement de plongée et sur les caractéristiques de leur environnement. Notre étude a mis en évidence une forte plasticité comportementale interspécifique qui semble être principalement dictée par les traits reproducteurs, les stratégies de reproduction, les conditions locales de l'habitat ou encore les adaptations physiologiques.

Mots clés : tortue olivâtre ; tortue verte ; tortue luth ; Atlantique équatorial ; comportement d'alimentation ; inter-ponte ; migration

Résumé en anglais

The strong heterogeneity of the marine ecosystem leads to a patchy distribution of the resources in time and space, shaping therefore the movements of sea turtles. Considered as the most dynamic ecosystem in the world, the Guiana shield is a highly dynamic system which hosts three of the seven sea turtle species in the world (the olive ridley, the green turtle and the leatherback turtle). The aim of this thesis was to understand how the oceanographic constraints can influence the at-sea movements of these three species during the reproduction and the migration phases. The deployment of 55 satellite tags on adult females in French Guiana provided information on their trajectories, their diving behavior and on the environment encountered. Our study shows a strong behavioral plasticity between species, which seems to be mainly dictated by the reproductive traits and strategies, the local conditions of the habitat and the physiological adaptations.

Keywords : olive ridley ; green turtle ; leatherback turtle ; equatorial Atlantic ; foraging behavior ; inter-nesting ; migration