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Caractéristiques maternelles, performances et stratégies de reproduction des tortues marines de Guyane

Virginie Plot

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ÉCOLE DOCTORALE des Sciences de la Vie et de la Santé

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THÈSE présentée par :

Virginie PLOT

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Discipline/ Spécialité : Sciences de la vie - Ecologie

**Caractéristiques maternelles,
performances et stratégies de reproduction
des tortues marines de Guyane**

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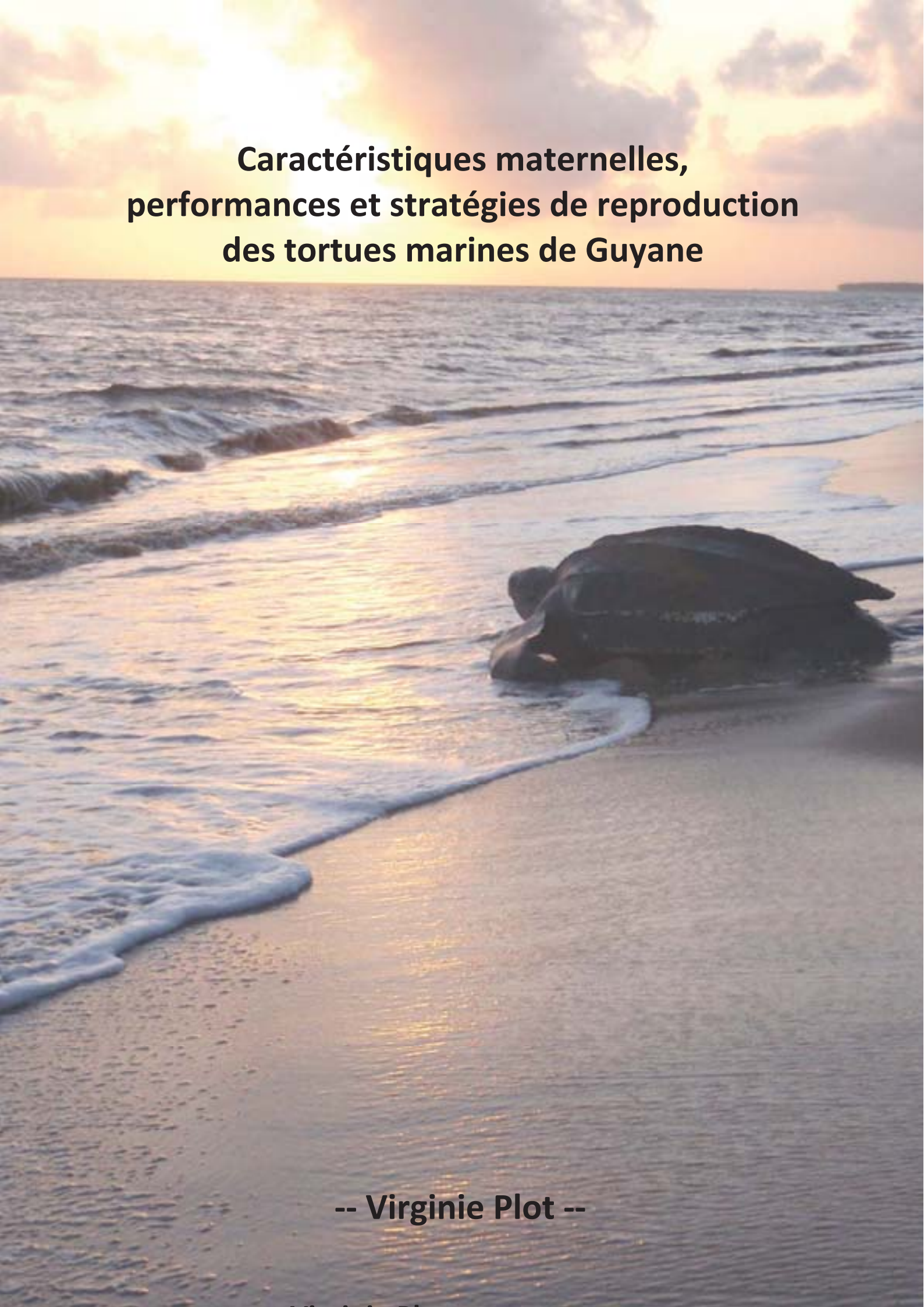
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A large sea turtle is resting on a sandy beach at sunset. The sun is low on the horizon, casting a warm, golden glow over the scene. The ocean waves are gentle, and the sky is filled with soft, colorful clouds. The turtle is the central focus, positioned in the lower right quadrant of the frame. The overall mood is peaceful and serene.

**Caractéristiques maternelles,
performances et stratégies de reproduction
des tortues marines de Guyane**

-- Virginie Plot --

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Dans une dimension lointaine et passablement farfelue, les tourbillons de brumes stellaires frémissent et s'écartent... Voyez... La tortue la Grande A'Tuin apparaît, elle fend d'une brasse paresseuse l'abîme interstellaire, ses membres pesant recouverts d'une givre d'hydrogène, son antique et immense carapace criblée de cratères météoritiques. Elle porte sur son dos quatre éléphants, eux-mêmes soutenant de leurs épaules le Disque-Monde. De ses yeux vastes comme des océans, encroûtés de chassie et de poussière d'astéroïdes, elle fixe le But Ultime... elle seule sait où elle va...

D'après les Annales du Disque-Monde, de Terry Pratchett. Dessin de Paul Kibdy, <http://www.paulkibdy.net/>

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1. INTRODUCTION



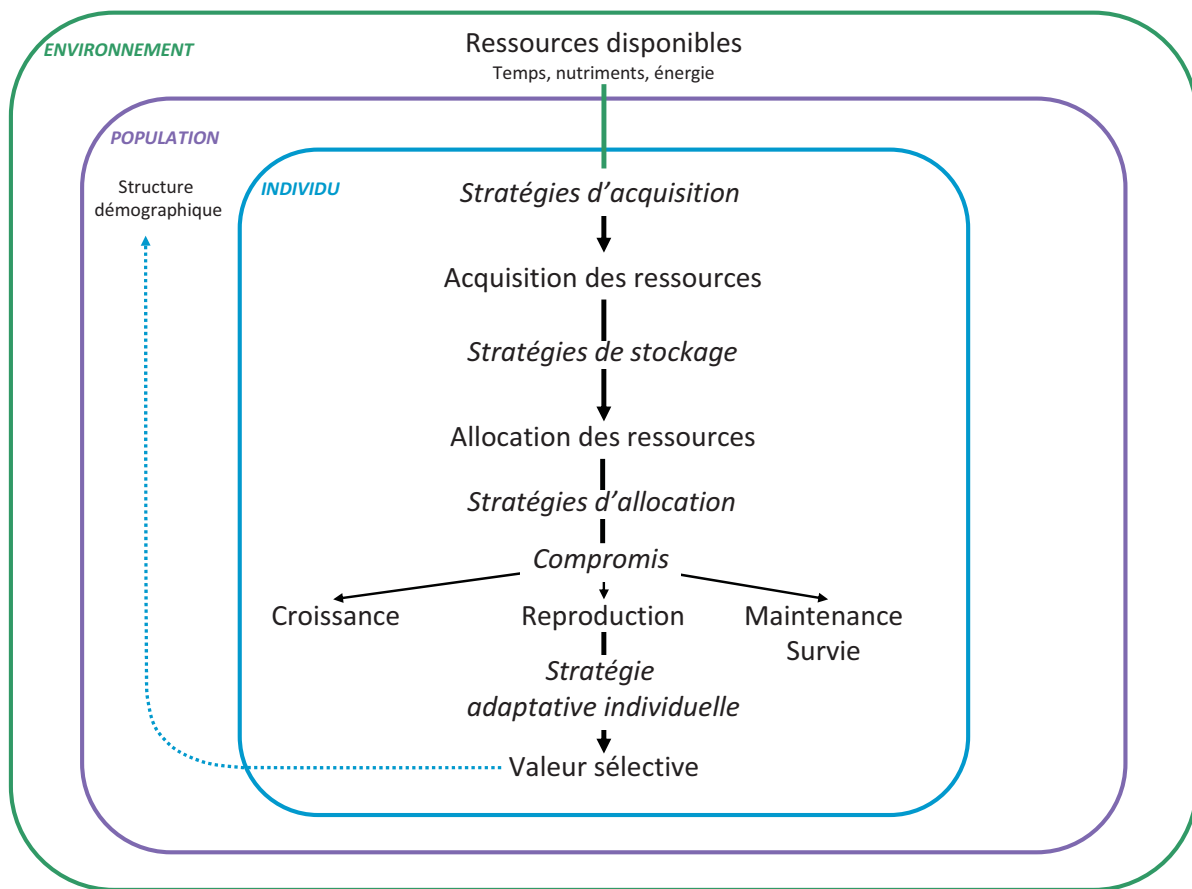


Figure 1.1. Tout organisme acquiert de l'énergie, la stocke puis l'alloue aux différentes fonctions de vie concurrentielles, qui sont la croissance, la maintenance, la reproduction et la survie. Les ressources disponibles dans l'environnement étant limitées dans le temps et dans l'espace, leur allocation vers une fonction se fera aux dépens des autres, contraignant ainsi les organismes à réaliser des compromis. La théorie des traits d'histoire de vie prédit qu'un compromis optimal doit émerger de sorte que la valeur sélective individuelle soit maximale, modelant ainsi les stratégies adaptatives individuelles. En retour, ces stratégies agissent sur la structure démographique des populations.

"The life history is similar to a pie divided into slices, each slices being devoted to a different function, such as growth, maintenance, storage or reproduction. Because the pie is of fixed size, increasing the size of a given slice necessarily decreases the size of another slice" Reznick et al. 2000

1. Contexte général : la théorie des traits d'histoire de vie

On appelle « **traits d'histoire de vie** » l'ensemble des caractères d'un organisme lui permettant d'assurer ses grandes fonctions de vie, qui sont la **croissance**, la **maintenance**, la **reproduction** et la **survie**. Les traits permettant une exploitation optimale de l'environnement sont sélectionnés et transmis *via* le génotype aux générations futures, par l'action de la sélection naturelle (Darwin 1859), le but ultime de tout organisme étant de transmettre son génotype aux générations suivantes, ou en d'autres termes, de maximiser sa **valeur sélective** (ou *fitness*, Stearns 1976).

Toutefois, l'environnement naturel étant hétérogène dans le temps et dans l'espace, les ressources (temps, énergie, eau, nutriments, *etc.*) sont fluctuantes et limitées. Selon le principe d'allocation, la ressource allouée à une fonction est nécessairement utilisée aux dépens des autres fonctions (Williams 1966, Levins 1968, Sibly & Calow 1986, Stearns 1989, Stearns 1992, Reznick *et al.* 2000). La **théorie des traits d'histoire de vie** propose que les organismes réalisent des **compromis** dans l'allocation des ressources vers les grandes fonctions de vie (Stearns 1992, **Fig. 1.1**). Les organismes adoptent donc des **stratégies adaptatives** qui résultent des meilleurs compromis et qui visent à maximiser leur valeur sélective. Ces compromis dits physiologiques (*sensus* Stearns 1992) sont sélectionnés au niveau de la population si une variation génétique y est associée ; on parle alors de **compromis évolutifs** (*sensus* Stearns 1992). Enfin, les stratégies adaptatives adoptées par les organismes agissent sur la dynamique de la population et de manière ultime sur la survie de l'espèce. Ces stratégies d'histoire de vie opèrent à différents niveaux ; elles peuvent être d'ordre écologique, comportemental, physiologique et/ou cellulaire (Wikelski & Ricklefs 2001, Le Maho 2002). L'étude des traits d'histoire de vie implique donc une approche intégrative de ces différents niveaux d'organisation.

Face à ces différentes contraintes, les organismes font face à une série de « décisions ». C'est à la suite du processus de décision qu'une stratégie est définie. Dans un premier temps, les **stratégies d'acquisition des ressources** (**Fig. 1.1**), concernent la répartition de l'effort de prospection dans le temps et dans l'espace, le choix des proies et le temps passé à s'alimenter. La théorie de l'approvisionnement optimal (*Optimal foraging theory*) prédit que l'activité de recherche alimentaire est profitable tant que le gain énergétique est supérieur à la dépense nécessaire pour obtenir ce gain (Mc Arthur & Pianka 1966, Charnov 1976, Stephens & Krebs

1986). Une fois acquises, les ressources alimentaires sont transformées lors de la digestion, où des compromis opèrent afin de maximiser le taux d'assimilation (Théorie de la digestion optimale, *Theory of optimal digestion*, Sibly & Callow 1986). L'énergie ainsi obtenue sera stockée, à plus ou moins long terme, selon la **stratégie de stockage des ressources** adoptée (**Fig. 1.1**).

Brown *et al.* (2004) ont proposé une théorie basée sur le métabolisme des organismes : *the metabolic theory of ecology*. Le métabolisme est le mécanisme biologique par lequel l'énergie et la matière sont transformées dans l'organisme. Par conséquent, le métabolisme détermine les besoins en ressources de l'organisme et crée de fortes contraintes d'allocation des ressources vers les grandes fonctions de vie. Par ailleurs, le métabolisme obéit aux principes physiques et chimiques qui gouvernent la transformation de l'énergie et de la matière (lois d'équilibre de masse et d'énergie, de la thermodynamique). On peut ainsi considérer que les traits d'histoire de vie des organismes sont contraints par les composants chimiques intervenant dans les voies métaboliques, mais également leur températures opérationnelles, leur taille corporelle, etc. (Brown *et al.* 2004).

Le but de tout organisme étant de transmettre son patrimoine génétique aux générations futures, l'étude des stratégies adaptatives associées à la reproduction est centrale à la compréhension de la variation des traits d'histoire de vie.

2. La reproduction

Classiquement, on distingue les organismes ne se reproduisant qu'une seule fois dans leur vie (semélipares) de ceux ayant plusieurs occasions de se reproduire (itéropares) (Cole 1954). Chez les organismes itéropares, le nombre d'épisodes reproducteurs réalisés au cours de la vie dépend de nombreux facteurs, dont notamment la durée de vie (organismes à vie courte dits courtévifs *vs* organismes à vie longue dits longévifs), la fécondité, la fréquence de reproduction qui caractérisent la reproduction. Ici, nous considérerons les organismes itéropares.

Un ensemble de termes associés à la reproduction sont définis dans la **Boîte 1.1**.

Boîte 1.1 Définitions de termes associés à la reproduction

Performance reproductrice : (*reproductive output*) : la production de la progéniture issue de la reproduction d'un individu. *e.g.* : le nombre de jeunes produits lors d'un épisode reproducteur.

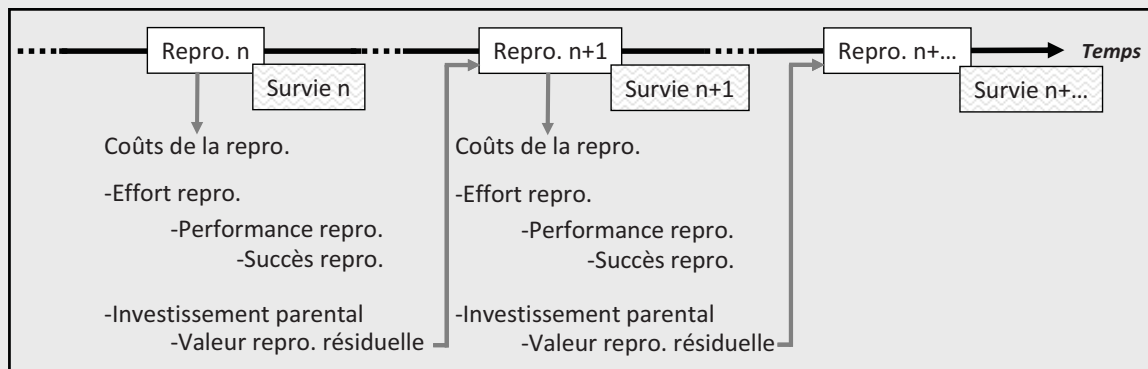
Effort de reproduction : la proportion des ressources qu'un individu alloue à la reproduction en cours (Hirshfield & Tinkle 1973).

Succès reproducteur : la proportion viable de la progéniture produite au cours d'un épisode reproducteur.

Coûts de la reproduction : coûts associés à la production de la progéniture, et aux soins qui lui est apportés, cumulés par un individu lors d'un épisode reproducteur et/ou de sa vie reproductrice.

Investissement parental : le degré auquel les ressources allouées à la progéniture (soins parentaux) diminuent la valeur reproductrice résiduelle des parents (Clutton-Brock 1991).

Valeur reproductrice résiduelle : la capacité d'un individu à se reproduire à nouveau (Williams 1966).



2.1. Les coûts de la reproduction

Au cours de la vie d'un organisme, la reproduction est considérée comme une période très coûteuse en énergie. Les coûts de la reproduction sont ainsi considérés comme une contrainte majeure qui détermine la réalisation de compromis adaptatifs aboutissant à l'adoption d'une stratégie de reproduction (Williams 1966, Clutton-Brock 1998).

Deux sortes de coûts de la reproduction ont été décrits : les **coûts directs** intervenant avant la libération des gamètes et les **coûts d'absorption** intervenant après la libération des gamètes (Sibly & Callow 1986). Selon ces auteurs, les coûts directs peuvent provenir (1) d'une augmentation des risques associés à la formation des couples et à l'accouplement

(comportements agressifs des compétiteurs sexuels ou visibilité accrue par les prédateurs) ; (2) d'une augmentation de l'effort de prospection alimentaire pour obtenir les ressources nécessaires à la production des gamètes et/ou à la préparation du nid ; (3) d'une distension morphologique et d'un déséquilibre mécanique causés par l'accumulation des gamètes, augmentant les besoins métaboliques et les risques de mortalité et/ou (4) d'une transformation des ressources des tissus somatiques vers la production des gamètes et les processus associés. Toutefois, ce coût peut-être réversible (*e.g.* la réabsorption des gamètes par le parent suite à un stress).

Les coûts d'absorption résultent quant à eux (1) des risques liés à la parturition (blessure ou augmentation de la vulnérabilité à la prédation ou aux maladies); (2) de l'épuisement des réserves propres à la maintenance des parents ; (3) de l'accumulation des effets néfastes liés au stress métabolique associé à la reproduction et / ou (4) de l'augmentation des coûts métaboliques et des risques de mortalité des parents associés aux soins apportés à la progéniture.

Chez certaines espèces animales, les **soins parentaux** peuvent ainsi constituer une part majeure des coûts de la reproduction. Les soins parentaux sont définis comme toute forme de comportement parental qui augmente la valeur sélective de la progéniture (Clutton-Brock 1991). On différencie les **soins parentaux pré-nataux et post-nataux**. Les soins parentaux pré-nataux incluent la préparation du nid ou du terrier, la production de grandes quantités d'énergie disponibles pour la progéniture (*e.g.* le vitellus de l'œuf) et / ou les soins apportés à la progéniture à l'intérieur du corps du parent (cas de la viviparité et de l'ovoviviparité) ou à l'extérieur du corps du parent (*e.g.* incubation). Les soins post-nataux consistent, quant à eux, à l'approvisionnement des jeunes après la naissance et / ou à la surveillance de la progéniture avant et après qu'ils soient indépendants du point de vue nutritionnel. Les bénéfices des soins parentaux reposent sur le rapport entre l'investissement parental et la valeur sélective de la progéniture. Pour de nombreuses espèces animales, chez qui les soins parentaux post-nataux sont absents, la production des gamètes représente le principal effort parental.

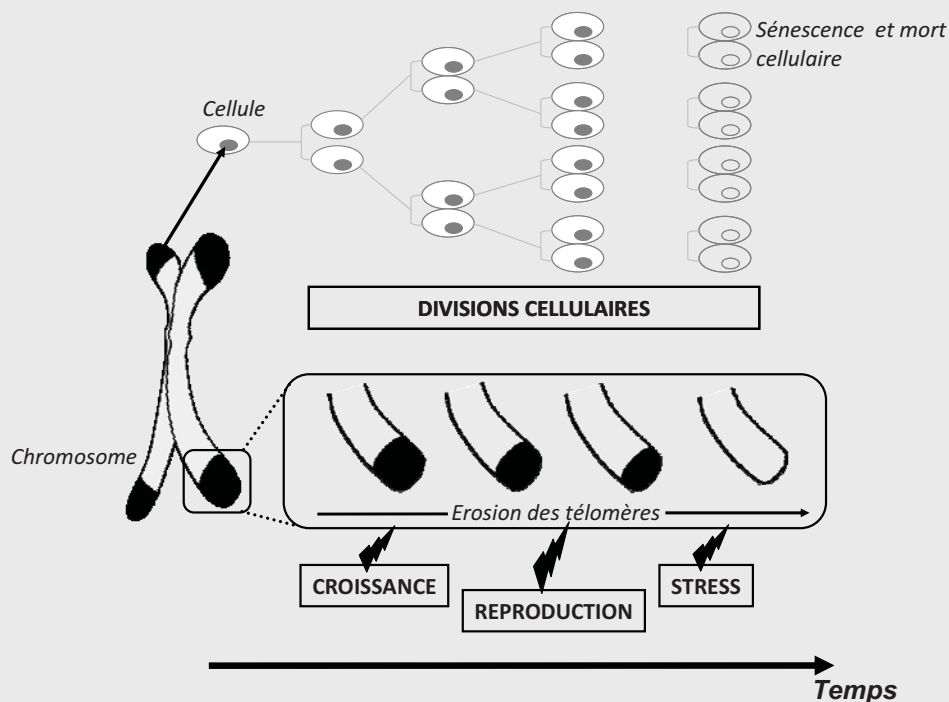
Les coûts de la reproduction peuvent se répercuter à différentes échelles. Par exemple à l'échelle de l'organisme, induisant une dépense énergétique importante, ce qui peut s'exprimer par une **dégradation de la condition corporelle parentale**. Ces coûts peuvent aussi se répercuter à l'échelle moléculaire, en induisant un stress oxydatif qui peut s'exprimer par le **raccourcissement** de l'extrémité des chromosomes qu'on appelle **des télomères** (Von

Zglinicki 2002, Metcalfe & Alonso-Alvarez 2010 ; Boîte 1.2.). Ainsi, les coûts de la reproduction s'expriment à différents niveaux d'intégration : ils peuvent aller du niveau physiologique au niveau démographique. Ils peuvent donc s'exprimer avec un certain décalage temporel, dans la mesure où ils ont un impact sur la survie ou la valeur reproductrice résiduelle des adultes (Clutton-Brock 1998, Rose & Bradley 1998).

Boîte 1.2. Les télomères

Les télomères sont des séquences répétitives d'ADN non codant, très conservées, qui chapeautent l'extrémité des chromosomes des cellules eucaryotes. Au cours des divisions cellulaires les télomères raccourcissent à cause du problème de réplification d'un brin d'ADN à l'extrémité 5'→3' (Blackburn 1991). Quand les télomères atteignent une longueur critique, et en l'absence d'une réponse appropriée du système de réparation de l'ADN (*via* la télomérase, *i.e.* l'enzyme qui restaure les télomères), la réplification s'arrête, déclenchant la fin de la division cellulaire, entraînant alors la sénescence puis la mort cellulaire (Blackburn 2000).

D'autre part, Les télomères sont sensibles au stress qu'un individu expérimente au cours de sa vie (e.g. Epel *et al.* 2004), et leur diminution de taille est particulièrement reliée au stress oxydatif (Von Zglinicki 2002). Le stress oxydatif est causé par le déséquilibre entre la production de molécules oxydantes et la capacité anti-oxydante de l'organisme. Il peut être induit par la croissance (e.g. Geiger *et al.* 2012), la reproduction (*i.e.* coûts de la reproduction, Metcalfe & Alonso-Alvarez 2010) ou des perturbations exogènes (e.g. Beaulieu *et al.* 2011).



2.2. Compromis associés à la reproduction

L'expression des compromis considère plusieurs paramètres associés à deux classes d'âge (juvénile et adulte): le temps jusqu'à la première reproduction (période de croissance), la survie juvénile, la fécondité, le temps entre deux épisodes reproducteurs, la survie adulte et la valeur sélective (Sibly & Callow 1986). En l'absence de contraintes, la valeur sélective est maximisée si la fécondité, la survie adulte et la survie juvénile sont maximisées et si le temps jusqu'à la première reproduction (*i.e.* l'âge de maturité sexuelle) et le temps entre deux épisodes reproducteurs sont minimisés. Hors, comme nous l'avons vu, des contraintes s'exercent sur les organismes et induisent des compromis entre les différents composants de leur valeur sélective. On différencie ainsi les compromis inter-individuels, qui concernent le reproducteur, et inter-générationnels, qui concernent le reproducteur et sa progéniture (Stearns 1992). Par soucis de simplification, les compromis sont combinés par paire de paramètres, les plus étudiés étant les suivants :

- Croissance juvénile vs reproduction

La croissance est le processus par lequel un organisme grandit de manière structurelle (taille, masse) et fonctionnel (*e.g.* développement de l'appareil reproducteur). Le compromis croissance-reproduction détermine combien un organisme est supposé investir dans la croissance avant d'investir dans la reproduction. En d'autres termes, il définit à quelle vitesse et jusqu'à quand il est le plus bénéfique de grandir avant la première reproduction et correspond à l'âge de maturité sexuelle ou à l'âge auquel la reproduction sera maximale (Bell 1980). De manière générale, il paraît idéal de maximiser le taux de croissance juvénile afin de minimiser le temps investi dans le développement et par conséquent de se reproduire aussi vite que possible. Une croissance rapide permet d'écourter les stades de vie pendant lesquelles les organismes sont les plus vulnérables (car plus petits), réduisant les risques de prédation et maximisant donc les chances de survie juvénile (Sibly & Callow 1986, Metcalfe & Monaghan 2003). De plus une croissance rapide peut augmenter le succès reproducteur (Metcalfe & Monaghan 2003). Toutefois, une croissance rapide peut avoir des effets négatifs notamment sur la longévité (Metcalfe & Monaghan 2003). Par ailleurs, l'âge de maturité sexuelle peut également être retardé si la fécondité augmente avec l'âge, augmentant ainsi le temps de croissance juvénile (Bell 1980).

Enfin, il faut noter le cas des organismes à croissance indéterminée, pour lesquels la croissance continue à l'âge adulte, bien que celle-ci soit moins importante après la première reproduction (voir section 4.4).

-Reproduction en cours vs survie adulte

Un corollaire de la théorie de l'allocation est que la reproduction constitue un coût pour la survie individuelle (Stearns 1992). En conséquence, l'importance de l'effort reproducteur par épisode reproducteur et le nombre d'épisodes reproducteurs au cours de la vie (fécondité) affectent les chances de survie des parents. Ainsi la seméliparité peut être interprétée comme un cas extrême de ce compromis entre reproduction et survie. Les soins parentaux peuvent également avoir des conséquences importantes sur la survie. Aussi, il existe chez certains organismes des signaux physiologiques induits par des hormones (notamment des glucocorticoïdes) qui déclenchent l'abandon de la reproduction en cours en faveur de la survie du parent (*e.g.* Spée *et al.* 2010).

- Reproduction en cours vs reproductions futures

Théoriquement, on prédit que tout épisode de reproduction est associé à un coût envers les chances de reproductions futures (Williams 1966, Callow 1979). En effet, une corrélation négative est supposée exister entre l'effort reproducteur d'un événement de reproduction et la valeur reproductrice résiduelle des parents (Fisher 1930).

L'hypothèse de l'investissement terminal propose que plus la valeur reproductrice résiduelle diminue, plus l'investissement en cours dans la progéniture augmente, résultant en une augmentation relativement importante de l'énergie dépensée dans la reproduction en fin de vie (Clutton-Brock 1984, ou modèle de reproduction optimale, Pianka & Parker 1975). Ainsi, plus le succès reproducteur futur attendu diminue et plus l'effort reproducteur du moment augmente. A l'inverse, l'hypothèse de sénescence prédit une diminution de l'effort reproducteur en raison d'une perte progressive des fonctions physiologiques et d'une dégradation générale de l'organisme dues au vieillissement. Ce déclin physiologique limiterait les capacités du parent à s'investir dans la reproduction à mesure qu'il vieillit (Clutton-Brock 1984).

Les approches comparatives inter-espèces suggèrent que la durée de vie des espèces (longévif ou courtévif) détermine les compromis entre reproduction courante et reproduction future en terme de taille/nombre de la progéniture (*e.g.* Chastel *et al.* 1995a). Par exemple, chez les espèces longévives, un individu qui aura par définition de nombreuses occasions de se reproduire, devrait, s'il est en mauvaise condition, réduire son effort reproducteur afin de préserver sa survie et donc ses reproductions futures (Goodman 1974, Clutton-Brock 1991).

- Nombre vs taille de la progéniture

Il est prédit que pour une quantité d'énergie donnée, la sélection naturelle devrait favoriser soit une progéniture nombreuse et de petite taille, soit une progéniture peu nombreuse mais de grande taille (Lack 1947, Smith & Fretwell 1974). Ce compromis est très différent selon les espèces et résulte en des variations très importantes des ratios [nombre de la progéniture/taille du parent] et [taille de la progéniture/taille du parent] (Stearns 1992). Si toutefois un surplus d'énergie est disponible, l'*optimal egg size theory* prédit que les parents devraient l'allouer de manière à produire une progéniture plus nombreuse plutôt qu'une progéniture de plus grande taille afin de maximiser sa valeur sélective (Smith & Fretwell 1974).

Ces compromis confrontant les fonctions de vie 2 à 2 restent toutefois schématiques. En effet, si l'on considère un individu reproducteur dans son environnement, celui-ci doit simultanément faire face à une combinaison des compromis énoncés ci-dessus. C'est de l'ensemble de ces compromis réalisés par un individu qu'émergera une stratégie individuelle de reproduction.

2.3. Influence des traits parentaux sur la reproduction

De nombreuses études montrent que le phénotype parental a un effet sur le phénotype de la progéniture et par voie de conséquence sur leur survie. Les traits parentaux considérés sont la taille, la masse, la condition corporelle du/des parents, mais aussi l'âge et l'expérience ou encore le comportement des parents. Ils peuvent influencer l'effort reproducteur, la performance de reproduction et le succès reproducteur des parents et à plus long terme la survie voire le succès reproducteur de la progéniture. Les traits parentaux peuvent donc être considérés comme une pression de sélection.

De manière générale, il est admis qu'au sein d'une même espèce, les organismes plus gros produisent une progéniture plus nombreuse, de meilleure condition et moins sujette à la prédation que les organismes plus petits (Stearns 1992). Drent et Daan (1980) soulignent également l'importance de la condition corporelle du parent au début de la reproduction comme indicateur du succès de cette dernière. Compte tenu de l'investissement prépondérant des femelles dans la reproduction, la plus grande partie des études s'est intéressée à l'influence des traits maternels. Ces études ont montré que la taille, la masse et/ou la condition corporelle des femelles affectent le succès reproducteur (*e.g.* chez la bernache cravant, *Branta bernicla* Ebbinge 1989, le pétrel bleu, *Halobaena caerulea* Chastel *et al.* 1995a, le manchot

Adélie, *Pygoscelis adeliae* Vleck & Vleck 2002), la taille, la masse et/ou le nombre de la progéniture (*e.g.* chez les serpents, Shine 2003, le requin sombre, *Carcharhinus obscurus* et le requin tisserand *Carcharhinus brevipinna* Hussey *et al.* 2010, le lézard à collier, *Crotaphytus collaris* Telemeco & Baird 2011), la survie de la progéniture (*e.g.* Hussey *et al.* 2010) ou encore le sexe de la progéniture (*e.g.* chez les mammifères, Trivers & Willard 1973). Enfin, les traits maternels tels que l'âge ou l'expérience peuvent également affecter la masse (*e.g.* chez la chèvre des Montagnes Rocheuses, *Oreamnos americanus* Côté & Festa-Bianchet 2012) ou la croissance (*e.g.* chez le sébaste noir, *Sebastes melanops*, Berkeley *et al.* 2004) de la progéniture, qui peut alors avoir un impact sur la survie juvénile.

De plus, bien que la contribution des mâles dans la reproduction se limite très souvent à la seule production des gamètes, chez certaines espèces animales, en particulier les oiseaux, les mâles participent à l'incubation et aux soins parentaux post-nataux. Les traits paternels peuvent donc également affecter la reproduction. Par exemple, chez le pétrel bleu, la condition corporelle paternelle affecte le succès reproducteur annuel (Chastel *et al.* 1995b).

Les études traitant de l'importance des traits parentaux caractérisent souvent les individus en termes de bonne ou mauvaise «qualité». Bien qu'importante, cette notion de qualité individuelle peut se révéler ambiguë (Wilson & Nussey 2010). Ces derniers proposent que la qualité est associée à l'hétérogénéité inter-individuelle et est corrélée positivement à la valeur sélective^{*}. La **qualité individuelle** reste toutefois difficilement mesurable (Wilson & Nussey 2010). Depuis quelques années, les études en écologie évolutive se sont intéressées à un nouvel outil moléculaire : les télomères (Monaghan 2010, **Boîte 1.2.**). En particulier, des études ont démontré que la variabilité inter-individuelle de la longueur des télomères et de leur taux de diminution de taille était positivement reliée à certaines composantes de la valeur sélective (*e.g.* Haussmann *et al.* 2003, Bize *et al.* 2009) dont notamment le succès reproducteur au cours de la vie (Pauliny *et al.* 2006). Ainsi, **la longueur des télomères représenterait un indicateur de la qualité individuelle.**

* “quality is an axis of among-individual heterogeneity that is positively correlated with fitness” (Wilson & Nussey 2010).

2.4. Influence des conditions environnementales sur la reproduction

Du fait des variations saisonnières, les ressources dans l'environnement ne sont pas disponibles à tout moment. Ainsi, la période de reproduction de nombreuses espèces coïncide avec la période où les conditions environnementales (*i.e.* régime thermique, ressources alimentaires) sont les plus favorables à la croissance et à la survie de la progéniture et à la restauration des réserves des adultes (*e.g.* Findlay & Cooke 1982, Rutberg 1984, Ogutu *et al.* 2010). Le climat agit ainsi comme agent de synchronisation des fluctuations des populations dans l'espace, également décrit comme l'effet Moran (Ranta *et al.* 1997).

L'optimisation de la reproduction consiste donc à ajuster l'effort de reproduction selon les conditions environnementales pour en limiter l'effet sur la survie adulte (Erikstad *et al.* 1998, Fig.1.3).

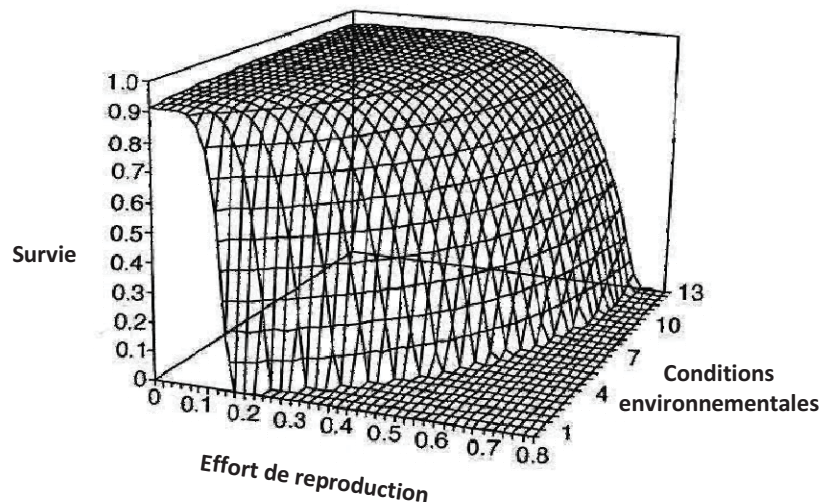


Figure 1.3. Influence des conditions environnementales sur l'effort de reproduction et la survie adulte (d'après Erikstad *et al.* 1998). Les parents doivent ajuster leur effort reproducteur en fonction de conditions environnementales pour assurer leur survie. Par exemple, à conditions environnementales constantes, une augmentation de l'effort reproducteur diminue la survie, et ce d'autant plus si les conditions environnementales sont défavorables

A une plus large échelle, de nombreuses études démontrent l'impact des changements climatiques (naturels et/ou anthropiques) sur la disponibilité alimentaire (*e.g.* Russell *et al.* 1971, Desmukh 1984, Fromentin & Planque 1996, Stenseth *et al.* 2003, Richardson & Schoeman 2004), avec des répercussions plus ou moins rapides sur le succès reproducteur (*match mismatch principle*, Durant *et al.* 2007). De plus, les changements environnementaux ont un impact sur la survie des adultes et/ou des juvéniles, et par voie de conséquence affectent les effectifs des populations (*e.g.* Stenseth *et al.* 2002, Drinkwater *et al.* 2003,

Suryan *et al.* 2009, Saraux *et al.* 2011). Les variations des conditions environnementales (abiotiques et biotiques), en affectant la condition corporelle des adultes, influencent les performances de reproduction. Récemment, Barrett *et al.* (2012) ont montré que le changement des paramètres climatiques (*i.e.* la température de la mer et l'oscillation Nord Atlantique) observé sur 30 ans est associé à une diminution de la taille des œufs chez le macareux moine (*Fratercula arctica*). Ils suggèrent que la diminution de l'abondance des proies de cet oiseau marin, causée par ces changements environnementaux, aurait modifié la condition corporelle des reproducteurs et aurait induit la production d'œufs de plus petite taille. De plus, les auteurs proposent que cette diminution de performance reproductrice résulterait en une progéniture de moindre qualité, ce qui pourrait à long terme, affecter de manière négative la population de macareux moine.

Enfin, l'influence des conditions environnementales diffère selon les caractéristiques intrinsèques des organismes: une distinction importante se fait entre les organismes endothermes qui subissent des effets indirects de l'environnement thermique et les organismes ectothermes qui subissent des effets directs de l'environnement. Face à cette variabilité environnementale, et à la diversité des traits d'histoire de vie, les stratégies de stockage des ressources trophiques destinées à la reproduction jouent un rôle majeur dans l'émergence des stratégies de reproduction.

3. Stratégies de stockage des ressources trophiques

3.1. Définition théorique

L'histoire de vie des organismes peut montrer des variations prononcées dans les voies de stockage de ressources destinées à la reproduction (Stephens *et al.* 2009). On considère deux grandes stratégies où les organismes sont définis comme des **reproducteurs sur capital** (*capital breeders*) ou des **reproducteurs sur approvisionnement** (*income breeders*). Drent & Dan (1980) introduisent ces concepts dans leur étude sur les déterminants de la reproduction chez les oiseaux. Ces auteurs comparent ces deux stratégies à des décisions économiques prises en termes d'investissement basé sur un capital déjà disponible ou sur des taux d'apport à un capital par le biais d'un revenu net quotidien. En termes biologiques, la reproduction sur capital repose sur des ressources stockées sous forme de réserves endogènes

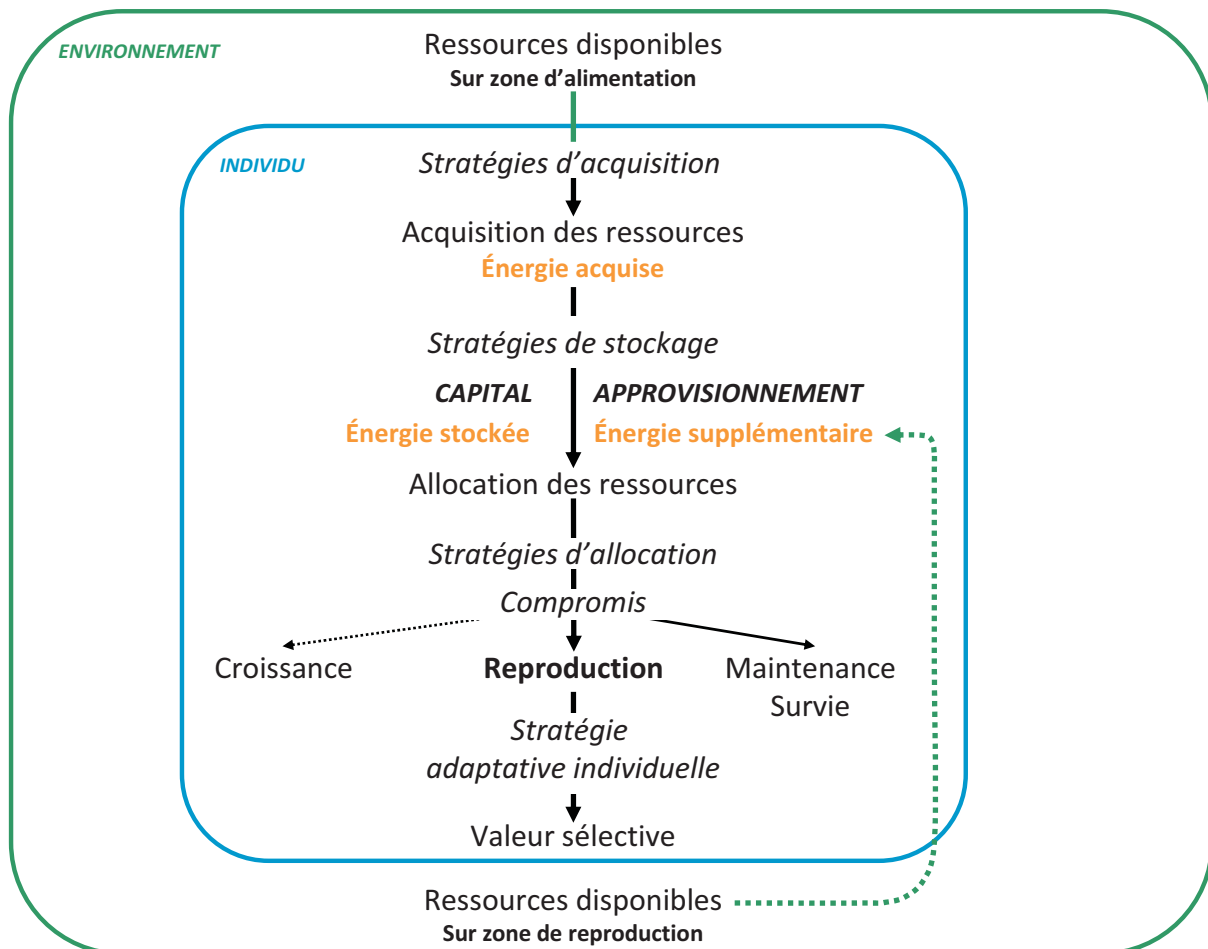


Figure 1.4. Les organismes utilisent différentes voies de stockage des ressources destinées à la reproduction décrites selon deux grandes stratégies: la reproduction sur capital et la reproduction sur approvisionnement. Alors que les reproducteurs sur capital utilisent de l'énergie stockée avant la reproduction pour mener à bien leur épisode reproducteur, les reproducteurs sur approvisionnement ajustent leurs besoins énergétiques en acquérant des ressources en cours de l'épisode reproducteur.

(*i.e.* capital) avant la période de reproduction. Au contraire, la reproduction sur approvisionnement est basée sur l'acquisition de ressources pendant la période de reproduction (*i.e.* réserves exogènes), alors allouées directement à la reproduction (**Fig. 1.4**).

Thomas (1988) précise que, chez les oiseaux, le capital représente une accumulation de nutriments déposés sous forme de réserves corporelles maternelles avant la ponte, qui est utilisée ultérieurement pour fournir les matériaux constituant les œufs. Les reproducteurs sur approvisionnement, quant à eux, ingèrent de la nourriture qu'ils dirigent rapidement dans la progéniture (Thomas 1988). Stearns (1992) accentue l'importance de l'énergie plutôt que des nutriments, comme la ressource clé pour laquelle les reproducteurs sur capital et sur approvisionnement montrent des différences quant aux stratégies de stockage. Toutefois, Bonnet *et al.* (1998) rappellent qu'en plus des réserves lipidiques et protéiques à partir desquelles le catabolisme fournit de l'énergie, les réserves de minéraux (comme le calcium ou le phosphore) stockées dans le squelette sont également à prendre en compte.

Selon la stratégie adoptée, les organismes vont faire face à une période de restriction alimentaire, ou de jeûne, plus ou moins longue. Face à cette contrainte, les organismes ont développé des mécanismes physiologiques adaptatifs, mis en évidence chez de nombreuses espèces (*e.g.*, Cherel *et al.* 1992, Robin *et al.* 1998, McCue 2007). Lors d'une période de jeûne, les organismes vont puiser dans leurs réserves corporelles suivant trois phases, correspondant à la mobilisation successive des différents substrats énergétiques endogènes (**Fig. 1.5**) : pendant la première phase, dite d'adaptation, ils vont utiliser les réserves glucidiques, illustré par une diminution de la glycémie. La deuxième phase, également appelée phase d'économie protéiques, correspond à la mobilisation des lipides. Cette phase est caractérisée par une diminution des triglycérides (TG) et également une augmentation du β -hydroxybutyrate. En dernier recours, les réserves protéiques sont mobilisées, avec l'augmentation de l'urée ou de l'acide urique. Si lors de la phase critique l'organisme ne peut pas se réalimenter, sa survie est mise en danger.

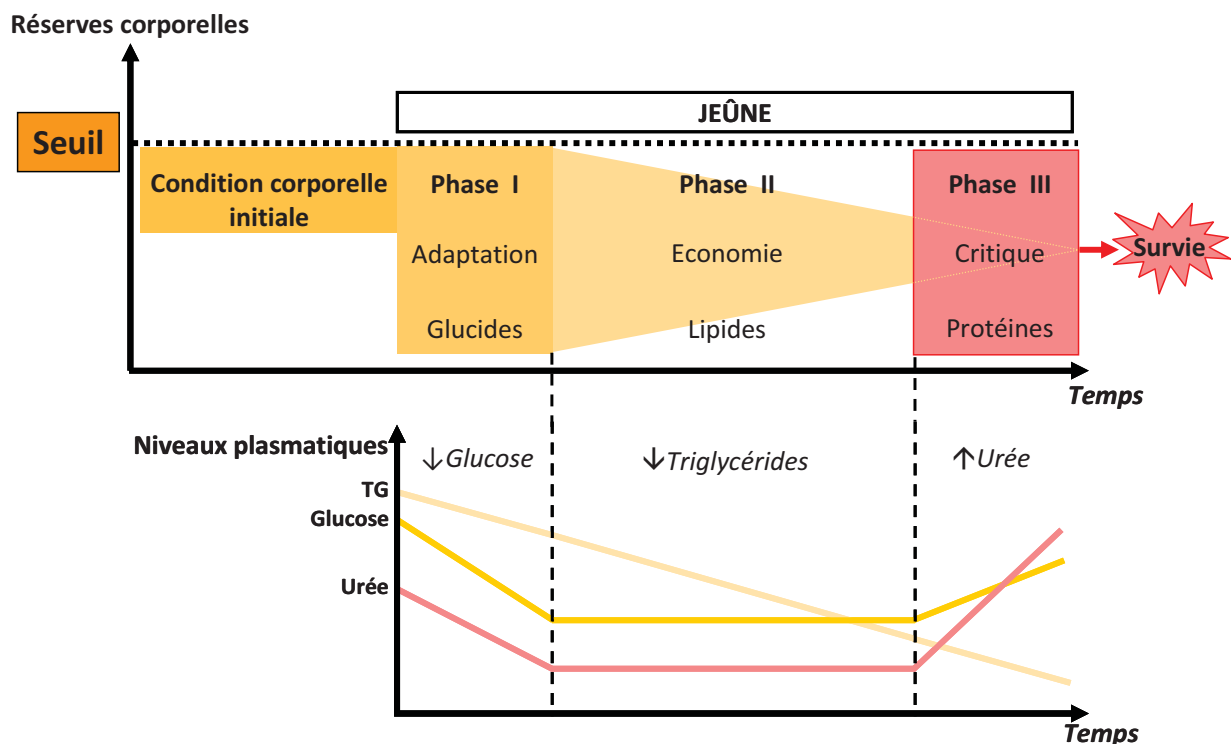


Figure 1.5. Schématisation de la mobilisation successive des différents substrats énergétiques endogènes et de la cinétique des concentrations plasmatiques de glucose, triglycérides (TG) et urée (ou acide urique) décrite lors du suivi longitudinal d'un individu au cours d'un jeûne prolongé.

3.2. Généralités

La stratégie de reproduction sur capital tend à être rencontrée chez les animaux de grande taille (relativement à la famille considérée), notamment chez les grands mammifères (Festa-Bianchet *et al.* 1998). Chez les pinnipèdes par exemple, les phoques et les éléphants de mer (famille des *Phocidés*), structurellement plus gros que les otaries et les lions de mer (famille des *Otariidés*), présentent une reproduction sur capital, alors que les derniers présentent une reproduction sur approvisionnement (Georges 2000, Boyd 2000, Houston *et al.* 2007). En effet, chez les phoques, il existe une séparation spatio-temporelle entre la période d'alimentation pendant laquelle les réserves maternelles sont accumulées et la période de reproduction où ces réserves sont transférées au jeune (gestation, période de lactation). Au contraire, les otaries alternent des voyages en mer durant lesquels elles se nourrissent et des visites à terre durant lesquelles elles allaitent leur jeune. Cette dichotomie dans les stratégies de stockage des ressources relative à la taille s'observe également chez les oiseaux. Par exemple, chez les anatidés arctiques, les plus grosses espèces comme l'oie des neiges (*Anser caerulescens*) utilisent les ressources accumulées lors de l'hivernage précédent pour subvenir

à la reproduction (Drent & Daan 1980, Drent *et al.* 2006), alors que les plus petites espèces comme les bécasseaux (*Calidridiines*) ou pluviers arctiques (*Charadriidés*) utilisent des ressources acquises sur le site de nidification (Klaassen 2001). Enfin, même chez des espèces d'invertébrés, on peut retrouver cette corrélation entre taille et stratégie de stockage des ressources ; en effet les reines des plus petites espèces de fourmis s'alimentent pendant la fondation de leur colonie alors que les reines des plus grosses espèces ne comptent que sur leurs réserves corporelles (Johnson 2006).

3.3. Avantages et inconvénients des deux stratégies

La reproduction sur capital implique une ségrégation spatio-temporelle prononcée entre les événements d'alimentation et de reproduction. Cela n'est pas le cas de la reproduction sur approvisionnement. On comprend donc facilement que les reproducteurs sur capital et sur approvisionnement sont confrontés à des contraintes différentes, dont découlent, pour chacun, des avantages (*i.e.* bénéfices) et des inconvénients (*i.e.* coûts) (**Tableau 1.1**).

La ségrégation spatiale permet aux individus d'alterner entre des habitats plus favorables à l'alimentation ou à la reproduction (Jönsson 1997). La ségrégation temporelle implique en premier lieu que la quantité de ressources capitalisées avant la reproduction est limitée. Ainsi, une mauvaise gestion de ce stock, à savoir des réserves en quantité insuffisante ou rapidement utilisées, peut compromettre la reproduction (Jönsson 1997). Toutefois, il a été montré que les reproducteurs sur capital présentent un seuil minimum de réserves corporelles nécessaire à l'engagement dans la reproduction, de sorte que l'épisode reproducteur en cours et la survie du reproducteur ne sont pas compromis (Drent & Daan 1980, Naulleau & Bonnet 1996, Boyd *et al.* 2000, Côté *et al.* 2012). Les reproducteurs sur approvisionnement, quant à eux, peuvent simultanément ajuster l'apport de ressources en fonction des besoins qu'ils rencontrent au cours de leur reproduction, ce qui leur confère une considérable flexibilité (Jönsson 1997). De plus, si les ressources alimentaires aux abords du site de reproduction sont abondantes, leur reproduction ne pourra en principe en être que meilleure ; cependant, si les ressources sont rares ou absentes, ils risquent de devoir abandonner leur reproduction. Au contraire, les reproducteurs sur capital, lors de l'établissement de leurs réserves, ont l'avantage de pouvoir tamponner les potentielles fluctuations environnementales en repoussant simplement leur prochaine reproduction. La ségrégation temporelle implique également une différence importante quant à la durée du stockage des ressources. En effet, un reproducteur sur capital va stocker ses réserves sur une période considérablement plus longues (plusieurs mois,

	Reproducteur sur capital	Reproducteur sur approvisionnement
Dissociation acquisition et allocation des ressources	plus	moins
Efficacité acquisition des ressources	plus	moins
Capacité à tamponner les fluctuations des conditions environnementales	plus	moins
Coûts énergétiques (stockage + allocation)	moins	plus
Capacités locomotrices pendant la reproduction	moins	plus
Risques de mortalité pendant la reproduction	moins	plus
Flexibilité des performances reproductrices	moins	plus

Tableau 1.1. Tableau comparant l'importance relative des critères caractérisant les stratégies de reproduction sur capital et de reproduction sur approvisionnement (plus/moins) et les avantages ou inconvénients (vert/rouge) qui en découlent de chacune.

voire plusieurs années) qu'un reproducteur sur approvisionnement qui utilise quasi immédiatement la ressource après l'avoir acquise. Jönsson (1997) stipule que stocker des ressources sur le long terme est d'un point de vue énergétique très coûteux pour l'organisme : en plus de l'énergie dépensée lors de leur acquisition, le maintien et la mobilisation ultérieure des réserves représentent des coûts énergétiques supplémentaires. L'auteur en déduit que la stratégie de reproduction sur capital représente un gaspillage d'énergie, et donc paraît moins efficace ou avantageuse que la stratégie sur approvisionnement (Jönsson 1997). Cependant, ce raisonnement ne tient pas compte, concernant les reproducteurs sur approvisionnement, des dépenses énergétiques associées à la digestion et aux processus impliqués dans la production du matériel nécessaire à la fabrication d'une progéniture, ni des dépenses énergétiques liées au stockage, bien qu'à court terme, des éléments transformés à l'issue de la digestion (Bonnet *et al.* 1998). Par conséquent, l'argument énergétique en défaveur de l'utilisation d'un capital est à remettre en perspective, en fonction des niveaux métaboliques spécifiques des organismes considérés (Bonnet *et al.* 1998, Brown *et al.* 2004).

Il existe par ailleurs des risques de mortalité différents associés aux deux stratégies. D'une part, à cause de ses importantes réserves, un reproducteur sur capital peut présenter une mobilité réduite résultant en un risque accru de prédation. D'autre part, un reproducteur sur approvisionnement devant s'alimenter en cours de reproduction s'expose à de potentiels prédateurs pendant la reproduction, ce qui peut l'amener à abandonner sa reproduction.

Les concepts de reproducteur sur capital et sur approvisionnement sont très utiles dans l'explication proximale de la diversité physiologique et comportementale des organismes (Stephens 2009). Cependant, de nombreuses études visant à comprendre quelle stratégie de stockage des ressources est employée par les organismes, basées sur une diversité d'espèces et différentes approches méthodologiques (voir **Boîte 1.3**), ont montré que certains organismes opèrent selon des **stratégies intermédiaires** (*e.g.* oiseaux : Drent *et al.* 2006, Sénéchal *et al.* 2009 ; mammifères : Bowen *et al.* 2001, Wheatley *et al.* 2008 ; reptiles : Lourdais *et al.* 2003, Warner *et al.* 2008). Ainsi, une vision plus complexe se dégage et considère l'existence d'un **continuum de stratégies** entre la reproduction sur capital et la reproduction sur approvisionnement (Drent & Daan 1980, Thomas 1988, Stearns 1989, Jönsson 1997, Bonnet *et al.* 1998). Ces stratégies intermédiaires résultent probablement d'une combinaison de facteurs liés aux coûts associés aux deux stratégies extrêmes et à la stochasticité des ressources trophiques.

Boîte 1.3. Méthodes pour définir les stratégies de stockage des ressources

1. Approches biochimiques et physiologiques

- **Suivi des réserves énergétiques endogènes parentales au cours de la reproduction :** Il est possible de réaliser le suivi de la composition corporelle du parent à différentes périodes de l'épisode reproducteur. Deux méthodes sont envisageables : (1) Analyser la composition en lipides et protéines des réserves d'individus sacrifiés à intervalles réguliers (2) Estimer la composition corporelle par dilution isotopique (*i.e.* technique de l'eau doublement marquée, Speakman 1997) d'individus suivis au cours de la reproduction.

- **Suivi du statut nutritionnel parental au cours de la reproduction :** La période de reproduction des reproducteurs sur capital peut être considérée comme une période de jeûne prolongé. L'utilisation des réserves corporelles associée à un jeûne à long terme est caractérisée par une mobilisation séquentielle des substrats énergétiques (Robin *et al.* 1998, **Fig. 1.5**). La mesure des niveaux plasmatiques des glucides, lipides et protéines constitue un bon indicateur du statut nutritionnel d'un organisme au cours de sa reproduction (Jenni-Eiermann & Jenni 1998). Les variations des ressources minérales, comme le calcium, entrant en jeu dans le développement de l'œuf et de l'embryon, peuvent également être mesurées au cours de la reproduction.

- **Estimation de la composition spécifique de la progéniture :** Les techniques d'analyse d'isotopes stables, permettent de caractériser un composant biologique par sa signature isotopique. Par exemple, la signature isotopique en ^{13}C et ^{15}N diffère selon un gradient terrestre/aquatique, marin côtier/marin océanique, marin pélagique/marin benthique et haute latitude/basse latitude (Hobson 1995, Kelly 2000,

Hobson 2006). Elle permet donc d'indiquer la provenance des ressources alimentaires, *i.e.* endogènes (maternelles) ou exogènes (apports nutritionnels), utilisées pour synthétiser les composants de la progéniture (œufs ou tissus).

2. Approche morphologique : Suivi biométrique au cours de la reproduction. Une diminution des réserves corporelles est associée à une perte de masse corporelle. On peut donc suivre la variation de la masse corporelle d'individus reproducteurs en effectuant des pesées régulières au cours de la reproduction. Ces mesures permettent également, si elles sont accompagnées de mesures structurelles (longueur, largeur du corps par exemple), de calculer un indice de condition corporelle reflétant l'état des réserves corporelles (Peig & Green 2009).

3. Approche comportementale : Estimation de la prise alimentaire en cours de reproduction. Grâce aux avancées technologiques et à la miniaturisation, des enregistreurs automatiques ont été développés pour estimer la prise alimentaire des animaux dans leur environnement. En particulier, les sondes œsophagiennes et les capteurs d'ouverture de bec (*Inter-mandibular sensors*) sont maintenant considérés comme étant des méthodes fiables pour évaluer à fine échelle les événements d'ingestion (*e.g.* Plötz *et al.* 2001, Wilson *et al.* 2002, Hanuise *et al.* 2010) et pour quantifier la prise alimentaire (Hanuise *et al.* 2010). Plus récemment, des enregistreurs de l'accélération tri-dimensionnelle ont été utilisés pour déterminer les tentatives/succès de prise alimentaire chez le manchot royal (*Aptenodytes patagonicus*, Hanuise 2011) et le lion de mer de Steller (*Eumetopias jubatus*, Viviant *et al.* 2010).

4. Les reptiles*

L'ectothermie confère une grande flexibilité des traits d'histoire de vie en fonction des conditions environnementales, grâce à la plasticité phénotypique ou aux adaptations (Shine 2005). En effet, à l'inverse des endothermes qui maintiennent une température interne relativement élevée et constante, les **organismes ectothermes** exploitent l'hétérogénéité thermique de l'environnement pour ajuster leur température interne, tout en ayant des coûts énergétiques (métaboliques) réduits en comparaison de ceux des endothermes. Ainsi, de manière générale, le métabolisme basal d'un ectotherme est six fois inférieur à celui d'un endotherme de taille similaire et à une même température (Bennett 1978). Parmi les ectothermes, les reptiles présentent sans doute la plus grande diversité de traits associés à la reproduction. Ils présentent différents modes de reproduction (seméliparité ou itéroparité ; oviparité, viviparité, pseudoviviparité, viviparité aplacentaire ou lécithotrophie, Blackburn 1994), de différenciation sexuelle ou de maturité sexuelle (Shine & Bonnet 2000, Shine 2003). De plus, les reptiles montrent d'importantes similitudes, qui en font un modèle privilégié pour l'étude comparative des traits d'histoire de vie (Shine 2003, Shine 2005).

4.1. Pré-disposition à la stratégie de reproducteur sur capital

La stratégie de reproducteur sur capital est particulièrement commune chez les ectothermes (Doughty & Shine 1998, Madsen & Shine 1999). En effet, il semblerait que les ectothermes, comme les reptiles, soient pré-adaptés à la stratégie de reproducteur sur capital (Bonnet *et al.* 1998). Premièrement, leur faible métabolisme induit des coûts de maintenance et de stockage d'énergie limités (Bonnet *et al.* 1998). D'autre part, la saison de reproduction est souvent brève et contrainte par les facteurs environnementaux (*e.g.* température du sol pour les reptiles ovipares), impliquant une ségrégation temporelle et spatiale marquée des épisodes d'alimentation et de reproduction (Shine 2003). De fait, la majorité des reptiles dépendent d'un important capital de réserves énergétiques pour leur reproduction (Bonnet *et al.* 1998, Shine 2005), qui implique que les femelles présentent un seuil de condition corporelle (Naulleau & Bonnet 1996) nécessaire pour s'engager dans la reproduction sans compromettre leur survie. Si les conditions environnementales sont peu favorables à l'élaboration de ce capital, les femelles peuvent reporter leur épisode reproducteur (Shine 2003). Toutefois, selon la qualité trophique de l'environnement, les femelles ajusteraient leur seuil de condition

* Selon la nouvelle classification, les lézards, les serpents, les crocodiles et les tortues sont des Sauropsidés, au même titre que les oiseaux (Lecomte 2006). Toutefois, désirant traiter des organismes uniquement ectothermes, nous parlerons de reptiles.

corporelle (Madsen & Shine 1999), voire, suite à de mauvaises conditions trophiques et malgré une condition corporelle relativement faible, compenseraient leurs réserves énergétiques insuffisantes par un apport alimentaire en cours de reproduction (Lourdais *et al.* 2002, Warner *et al.* 2007). Enfin, les ectothermes peuvent tolérer de longues périodes de jeûne, pouvant durer de plusieurs semaines à plusieurs mois, imposées par leur cycle de vie (*e.g.* pendant la période d'hibernation) (*e.g.* Voituron *et al.* 2000, Wang *et al.* 2006) ou par le fait de porter leur progéniture (Shine 2003).

4.2. Faible fréquence de reproduction

Parce que leur reproduction s'appuie sur d'importantes réserves corporelles, les reptiles sont caractérisés par une faible fréquence de reproduction (*Low frequency of reproduction*, Bull & Shine 1979). Selon Bull & Shine (1979), les espèces à faible fréquence de reproduction présentent des « activités accessoires » importantes associées à leur cycle reproducteur. Parmi ces activités sont citées les migrations, les soins/la défense de la progéniture et la rétention de la progéniture dans les voies génitales. Ces activités imposent des dépenses en temps et en énergie et/ou affectent la survie adulte et peuvent être indépendantes de la fécondité. Si les coûts associés à ces activités sont très élevés, l'organisme aura avantage à se reproduire de façon alternée, de manière à éviter ces coûts fixes et profiter d'une année de repos pour investir plus d'énergie et assurer un meilleur succès dans l'épisode reproducteur suivant. Ainsi le report d'un événement reproducteur peut maximiser à long terme (*i.e.* la durée de vie) le succès reproducteur (Schaffer 1974).

4.3. Absence de soins parentaux post-nataux

Chez les reptiles, les soins parentaux incombent aux femelles, et à quelques exceptions près, l'effort maternel peut se résumer aux soins prénataux (Clutton-Brock 1991). La plupart des espèces ovipares enterrent leurs œufs et ne surveillent pas le nid après. La surveillance des œufs par les femelles existe chez 3 % des espèces de serpents ovipares et 1 % des espèces de lézards ovipares mais dans toutes les espèces de crocodiliens (Shine 1988). Bien que les femelles pythons régulent la température du nid en produisant de la chaleur par frisson thermique, les soins parentaux post-éclosion sont également très rares chez les serpents (Shine 2003). Par conséquent **chez les reptiles, l'effort reproducteur correspond à la performance reproductrice** (nombre et taille de la progéniture, Congdon 1989, Bonnet *et al.*

1998), ce qui facilite la compréhension des coûts associés à la reproduction et donc des compromis sous-jacents.

4.4. Croissance indéterminée

Les ectothermes présentent une croissance indéterminée, *i.e.* la croissance continue après la maturité sexuelle. Il en résulte, qu'au stade adulte, un compromis supplémentaire existe entre la croissance et la reproduction (Stamps *et al.* 1998, Heino & Kaitala 1999). L'allocation des ressources dédiées à la croissance vers la reproduction entraîne des coûts pour la croissance, expliquant que les adultes ont une croissance moins importante que les immatures (*the growth costs of reproduction*, Stamps 1998). D'autre part, la taille d'un individu est un déterminant important du succès de reproduction s'il y a compétition pour l'accès aux ressources requises pour la reproduction ; on considère que l'individu le plus grand/gros a un succès plus important qu'un individu plus petit (Stamps 1998). De plus chez les reptiles, il existe une forte corrélation entre la taille de la femelle et les performances reproductrices (*e.g.* lézards : Olsson & Shine 1997, Du *et al.* 2005; serpents : Shine 2003 ; crocodiles : Guillette 2007; tortues: Rollinson & Brooks 2008). Ce lien repose sur les contraintes physiques associées à l'accumulation de réserves nécessaires pour la production de la progéniture, celles-ci dépendant du volume corporel de la femelle (Vitt & Congdon 1978). Par conséquent, allouer des ressources vers la croissance implique *a posteriori* une performance reproductrice plus importante. La stratégie optimale repose alors sur le fait d'allouer le surplus de ressources vers la croissance aussi longtemps que ce surplus favorise les futures reproductions (Kozlowski 1999). De façon intéressante, il a récemment été suggéré chez le lézard à collier (*Crotaphytus collaris*), qui réalise plusieurs pontes au cours d'un épisode reproducteur, que le capital de ressources est utilisé pour produire les œufs alors qu'un apport exogène (approvisionnement) est utilisé pour la croissance (Telemeco & Baird 2011).

4.5 Influence des traits maternels

En plus de la taille (cf paragraphe ci-dessus), la condition corporelle maternelle affecte considérablement la reproduction (*e.g.* Litzug *et al.* 2008, Telemeco & Baird 2011). Par ailleurs, les femelles ovipares peuvent influencer le succès de la reproduction et le phénotype de leur progéniture (Shine 2003). Par exemple, de faibles variations dans la composition du jaune de l'œuf, comme le niveau hormonal, peuvent modifier le développement de l'embryon

(Shine 2003). Le choix du site de ponte, *i.e.* la nature du substrat, les conditions hydriques et thermiques pendant l'incubation, peut également affecter le bon déroulement du développement embryonnaire, le phénotype ou même le sexe de la progéniture (*e.g.* Shine & Harlow 1996, Warner & Andrews 2000, Brown & Shine 2004, Rafferty & Reina 2012a).

Les reptiles constituent ainsi des modèles privilégiés pour l'étude des traits reproductifs et des compromis évolutifs associés.

4.6. Le cas des tortues marines

Les tortues marines sont des reptiles marins longévifs, à maturité sexuelle tardive (Chaloupka & Musick 1997), itéropares et ovipares, présentant une croissance indéterminée. A la différence de nombreux autres reptiles, les tortues marines présentent un mode de reproduction particulier, puisqu'au cours d'une même saison, elles produisent plusieurs pontes (jusqu'à 6 en moyenne) comptant chacune de nombreux œufs (Miller 1997, **Fig 1.6.**). Ce mode de reproduction résulte, probablement d'une importante et imprévisible mortalité pendant le stade œuf et les premiers stades de vie (Van Buskirk & Crowder 1994). De plus, les tortues marines présentent une ségrégation spatio-temporelle entre les événements d'alimentation et la reproduction : les femelles effectuent des migrations océaniques pluri-annuelles pendant lesquelles elles s'alimentent dans les zones subtropicales (voire tempérées) et rejoignent les plages des régions tropicales pour se reproduire. Ainsi, pendant toute la durée de la saison de ponte, les besoins énergétiques associés à leur reproduction sont entièrement assurés par les ressources acquises lors de leur migration. **Les tortues marines sont ainsi considérées comme des reproducteurs sur capital** (Miller 1997). Toutefois, de récentes études mettent en avant plusieurs éléments (biométriques ou comportementaux) supportant que **quatre des sept espèces de tortues marines adopteraient une stratégie intermédiaire**, où les femelles gravides s'alimenteraient (ou tenteraient de s'alimenter) pendant la saison de ponte sur certains sites de reproduction (tortue verte *Chelonia mydas* : Hochscheid *et al.* 1999; tortue imbriquée *Eretmochelys imbricata* : Santos *et al.* 2010; tortue caouanne *Caretta caretta* : Schofield *et al.* 2006; tortue luth *Dermochelys coriacea* : Eckert *et al.* 1989, Myers & Hays 2006, Fossette *et al.* 2008a).

Malgré un cycle de vie commun, les 7 espèces de tortues marines montrent des différences importantes : elles présentent une importante gamme de taille (de 55 à 178 cm de longueur de carapace à l'âge adulte, Spotila 2004, **Fig.1.6**), un régime alimentaire varié (herbivore, carnivore ou omnivore, Bjorndal 1997, **Fig.1.6**) et des schémas d'histoire de vie contrastés quant aux domaines écologiques exploités au cours de leur vie (Bolten 2003, Fossette 2008c, **Fig.1.6**). Enfin, bien qu'elles aient un mode de reproduction similaire, leur effort reproducteur présente une variabilité importante parmi les espèces, particulièrement chez la tortue luth (**Fig. 1.6**). Ainsi, les tortues marines présentent un modèle privilégié pour l'étude comparative des traits d'histoire de vie. Pourtant, à l'inverse des squamates, les tortues marines se révèlent être un modèle très peu étudié dans le contexte des traits d'histoire de vie et des compromis évolutifs associés.

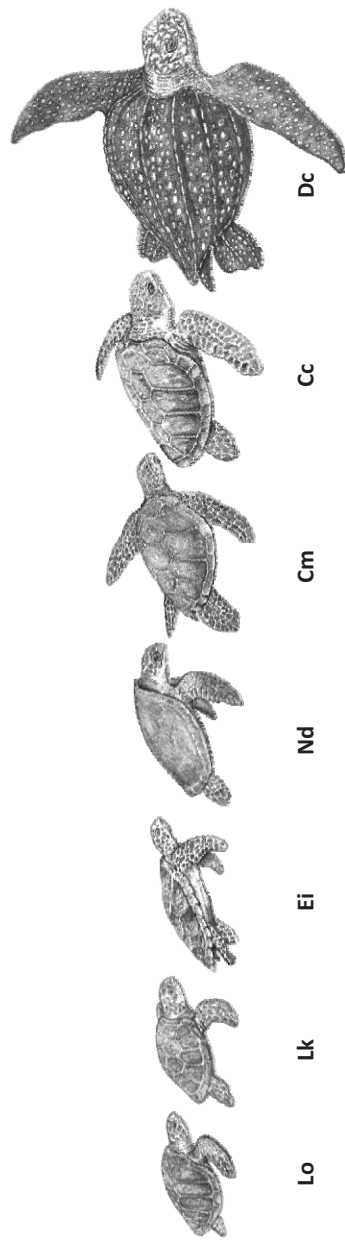
5. Objectifs, hypothèses et approches de travail

L'objectif de ce travail est de préciser les stratégies de reproduction chez les tortues marines. Il s'intéresse en particulier aux stratégies de stockage et d'allocation des ressources destinées à la reproduction chez les **tortues luth de Guyane** et repose sur plusieurs approches à différents niveaux d'intégration (*i.e.* morphologique, physiologique et moléculaire).

Nous nous sommes intéressés à la tortue luth, chez qui la stratégie de reproduction sur capital a été récemment remise en question. Pourtant, les tortues luth présentent les traits les plus caractéristiques d'une reproduction sur capital: la ségrégation spatio-temporelle entre alimentation et reproduction est très marquée puisque les zones d'alimentation qu'elles exploitent sont distantes de plusieurs milliers de kilomètres de leurs sites de reproduction ; elles présentent une faible fréquence de reproduction et de durée variable (de 2 à 8 ans) liée à la durée de la migration ; et leurs imposantes dimensions leur permettent l'établissement d'un capital important de réserves corporelles.

Nous proposons dans un premier temps de tester l'hypothèse nulle selon laquelle les tortues luth de Guyane opèrent comme des reproducteurs sur capital.

Dans ce cas :



	Lo	Lk	Ei	Nd	Cm	Cc	Dc
Taille adulte (cm)	55-76	61-76	75-88	75-99	80-122	85-124	132-178
Poids adulte (kg)	36-43	36-45	43-75	70-90	65-204	80-200	250-907
Alimentation (adulte)	Crustacés (+ algues)	Crabes	Eponges corail	Invertébrés benthiques	Algues, phanérogames	Poissons, invertébrés (+ algues)	Méduses, tuniciers
Habitats							
Développement	Néritique	Océanique	Océanique	Néritique	Océanique	Océanique	Océanique
Adulte	Océanique ou néritique	Néritique	Néritique	Néritique	Néritique	Néritique	Océanique et néritique
Reproduction							
Nb pontes/saison	2,21 ± 0,79	1,80 (—)	2,74 ± 0,22	2,84 (—)	2,93 ± 0,28	3,49 ± 0,20	6,17 ± 0,47
Nb œufs/ponte	109,9 ± 1,8	110,0 (—)	130,0 ± 6,8	52,8 ± 0,9	112,8 ± 3,9	112,4 ± 2,2	81,5 ± 3,6
Effort reproducteur x (Nbœufs/an/ind)	148,8 ± 4,7	132,0 (—)	122,8 ± 13,6	56,6 (—)	115,5 ± 4,7	151,4 ± 2,9	220,5 ± 12,0

Figure 1.6. Traits d'histoire de vie des 7 espèces de tortue marine. Lo, *Lepidochelys olivacea*, Tortue olivâtre; Lk, *Lepidochelys kempii*, Tortue de Kemp; Ei, *Eretmochelys imbricata*, Tortue imbriquée; Nd, *Natator depressus*, Tortue à dos plat; Cm, *Chelonia mydas*, Tortue verte; Cc, *Caretta caretta*, Tortue caouanne ; Dc, *Dermochelys coriacea*, Tortue luth. D'après Spotila 2004, Miller 1997, Bjørndal 1997, Bolten 2003 et Fossette 2008c (Source des dessins : www.seaworld.org).
 x Effort reproducteur = (Nb œufs/ponte) * (Nb pontes/saison) / durée migration.

H1- Pendant la période d'acquisition et de stockage des réserves, *i.e.* période de migration, les paramètres biométriques et morphologiques des femelles devraient montrer des différences importantes témoignant d'une stratégie de stockage (**Article 1**).

H2- Pendant la période d'allocation des réserves, *i.e.* au cours de la saison de ponte, les paramètres biométriques et physiologiques des femelles devraient suivre une cinétique semblable à celle décrite pendant un jeûne prolongé (**Article 2**) et témoigner de l'absence de prise alimentaire (**Article 3**).

Si ces deux premières hypothèses sont validées, alors :

H3- La performance de reproduction des femelles réalisée au cours d'une saison de ponte devrait être fortement reliés aux traits maternels (*i.e.* taille, masse et condition corporelle) en début de saison (**Article 2**). Ainsi on pourrait définir des indices de la qualité reproductrice individuelle (**Article 4**).

H4- La migration étant la période pendant laquelle les femelles stockent les réserves sur lesquelles repose leur reproduction, alors la durée et les conditions trophiques de la migration devraient influencer la prise de masse des femelles et/ou leur performance de reproduction (**Résultats préliminaires**).

En d'autres termes, nous avons cherché à répondre aux questions suivantes :

- Comment les tortues marines stockent-elles et gèrent-elles leurs réserves destinées à la reproduction?
- Comment les caractéristiques maternelles affectent-elles les performances reproductrices ?
- Quels sont les liens entre migration et reproduction des tortues marines ?

Après avoir présenté le site et le modèle d'étude, et les approches méthodologiques, nous présenterons une synthèse des principaux résultats de ce travail de thèse. Ces éléments de réponse seront ensuite discutés dans le cadre d'un contexte plus général des traits d'histoire de vie et des stratégies de reproduction puis des perspectives à ce travail seront proposées. Les articles issus de ce travail termineront ce mémoire.

2. METHODOLOGIE



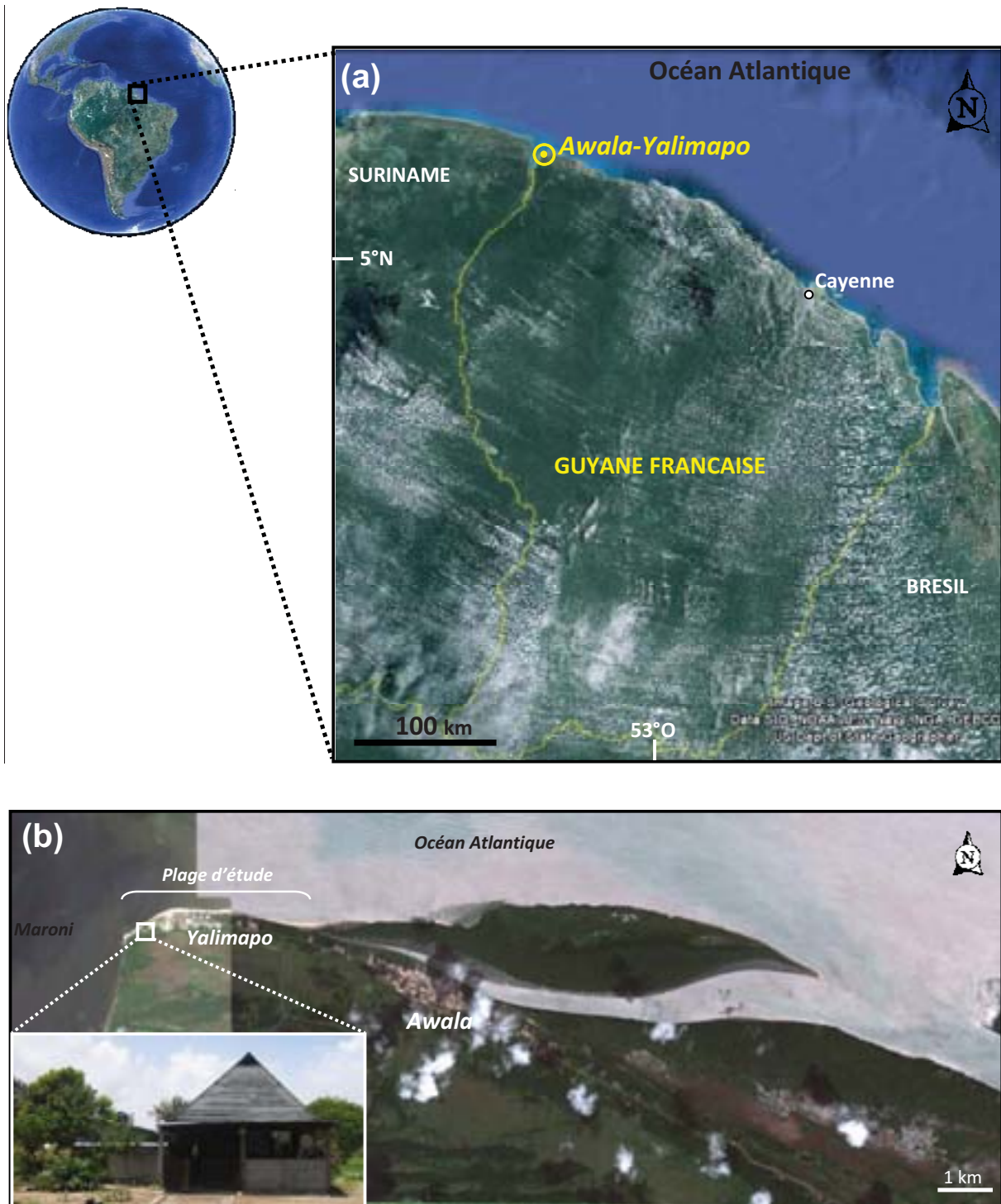


Figure 2.1. (a) Localisation du site d'étude (cercle jaune) à l'Ouest de la Guyane (Fig. 2.1). (b) La plage de Yalimapo ($53^{\circ}57' W / 5^{\circ}45' N$, Fig. 2.1) borde le village amérindien de Awala-Yalimapo situé à l'embouchure du Maroni, fleuve frontalier entre Guyane et Suriname. Notre carbet de terrain (insert) se situe dans le village de Yalimapo. (Fonds de carte Google Earth).

1. Site d'étude

La Guyane est un département français d'Amérique du Sud situé entre le Brésil et le Suriname (**Fig. 2.1.a**). Son littoral (d'environ 300 km) peu urbanisé, à l'exception des villes de Cayenne et Kourou, est parsemé de petits villages et hameaux, et alterne entre mangroves et plages de sable. Le climat est équatorial : toute l'année la température reste constante (en moyenne 26 °C), et le rythme des saisons n'est marqué que par l'alternance des saisons sèches (de mi-juillet à décembre et au mois de mars) et des saisons des pluies (janvier-février et d'avril à juillet).

2. Les tortues marines de Guyane

C'est vers la fin des années 1960 que Pritchard (1969) et Schultz (1971) décrivent pour la première fois l'importance internationale des sites de ponte de la région des Guyanes (Guyane-Suriname-Guyana). La Guyane constitue l'un des sites de ponte majeurs à l'échelle mondiale pour les tortues luth (Fossette *et al.* 2008b) et à l'échelle de l'Atlantique pour les tortues olivâtres (Kelle *et al.* 2009). On rapporte également sur les plages de Guyane la présence de la tortue verte, et de manière plus anecdotique, de la tortue imbriquée et de la tortue caouanne. Les deux plus importantes plages de ponte sont situées aux extrémités géographiques de la Guyane (**Fig. 2.1.a**) : à l'Est, l'île de Cayenne accueille majoritairement les femelles tortue luth et tortue olivâtre; à l'ouest, la plage de Yalimapo accueille une importante population de tortues luth et de tortues vertes, et constitue le site historique de l'étude des tortues marines en Guyane (Fossette *et al.* 2008b).

La démarche des institutions gouvernementales, des ONG et des scientifiques adoptée en Guyane concernant les tortues marines a été de focaliser les suivis sur les tortues luth, puis plus récemment sur les tortues à écailles (tortue olivâtre et tortue verte). Toutefois, l'état des connaissances sur les tortues vertes est quasi inexistant, puisque le suivi a démarré en 2010.

Ce travail de thèse s'est intéressé à l'étude de la reproduction des tortues luth sur la plage de Yalimapo (Fig. 2.1.b).



Figure 2.2. Une femelle tortue luth sortant de l'eau pour venir pondre sur la plage de Yalimapo. (© JY Georges).

Seule représentante de la famille des *Dermochelyidea*, la tortue luth (**Fig. 2.2**) se distingue des autres espèces de tortue marine (en plus de par sa taille, **Fig. 1.6**) par son anatomie, sa physiologie et sa répartition géographique. La tortue luth est la seule à ne pas avoir une carapace faite d'écailles kératinisées, mais possède une dossière constituée d'une mosaïque de petites plaques osseuses surmontée d'une épaisse couche de tissus conjonctif et adipeux recouverte d'une peau ayant l'aspect du cuir (Wyneken 2001). D'autre part, elle possède un métabolisme au repos trois fois supérieur à celui estimé pour un reptile de sa taille et moitié moindre que celui d'un mammifère de taille comparable (Paladino *et al.* 1990). Elle dispose d'une capacité à moduler le flux sanguin de ses tissus périphériques, lui permettant de thermoréguler (Greer *et al.* 1973, Spotila *et al.* 1997). Ces adaptations morphologiques et physiologiques particulières liées à la gigantothermie (Paladino *et al.* 1990) permettent à la tortue luth de maintenir une température corporelle largement supérieure (jusqu'à 18°C ; Frair *et al.* 1972) à celle du milieu où elle se trouve. Par conséquent, son aire de répartition s'étend jusqu'aux eaux tempérées froides des hautes latitudes (*e.g.* Ferraroli *et al.* 2004, James *et al.* 2005). Les tortues luth sont exclusivement planctonophages, leur régime alimentaire se composant essentiellement de méduses (Bjorndal 1997). La tortue luth partage le même cycle de vie que toutes les espèces de tortues marines (**Fig. 2.3, Boîte 2.1**)

Les tortues luth se reproduisant en Guyane réalisent des migrations de 2 ou 3 ans (Rivalan *et al.* 2005), au cours desquelles elles se dispersent dans tout l'Atlantique Nord (Ferraroli *et al.* 2004, Fossette *et al.* 2010a, **Annexe 1**) où elles exploitent différentes zones d'alimentation, océaniques et néritiques (Fossette *et al.* 2010a, **Annexe 1**). Trois zones majeures d'alimentation ont été rapportées : dans les eaux canadiennes près de la Nouvelle Ecosse, dans les eaux européennes, près des côtes françaises et britanniques et près des côtes ouest Africaines (Fossette *et al.* 2010a, **Annexe 1**). Les tortues luth réalisent le plus important effort reproducteur (Van Buskirk & Crowder 1994) et particulièrement celles de Guyane: un nid contient de 80 à 100 œufs d'environ 90 g chacun et certaines femelles réalisent jusqu'à 14 pontes pendant une saison de reproduction (Girondot & Fretey, 1996).

En Guyane, la saison de reproduction des tortues luth s'étend de début Mars à fin Juillet.

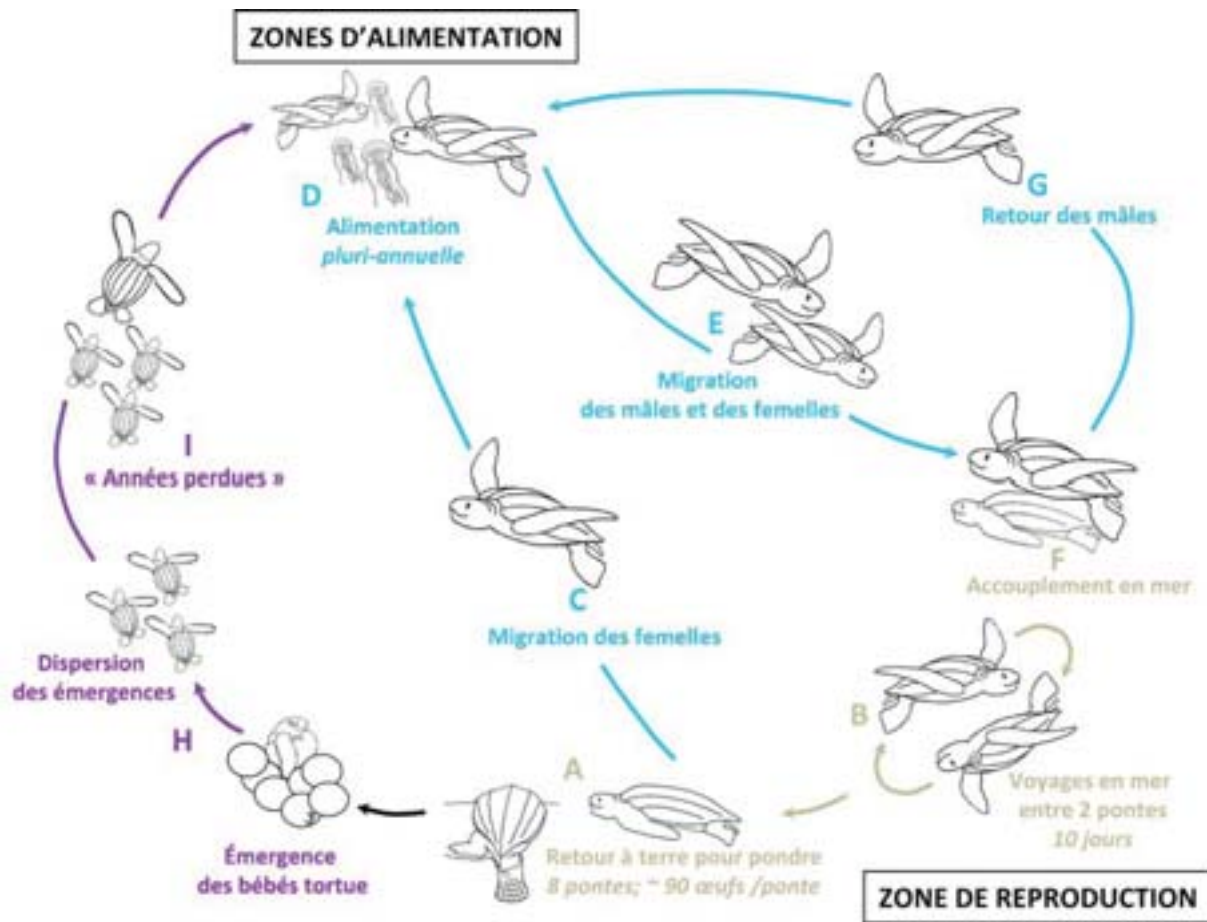


Figure 2.3. Cycle de vie des tortues marines. Les estimations des paramètres reproductifs indiquées en italique correspondent aux valeurs moyennes pour les tortues luth de Guyane (Girondot & Fretey 1996, Rivalan *et al.* 2006, cette étude). Les lettres A à I se réfèrent aux différentes phases du cycle, décrites dans la Boîte 2.1. Les couleurs distinguent les 3 grandes phases de vie : en violet, développement des jeunes immatures; en bleu, migrations en mer et en beige, période de reproduction.

Les tortues marines passent 99% de leur vie en mer. *“Sea turtles spend about as much time on land in their lives that you spend getting your hair cut.”* B. Wallace

Boîte 2.1. Cycle de vie des tortues marines

Pendant la saison de reproduction qui dure plusieurs semaines, les femelles viennent à terre déposer plusieurs pontes (de 2 à 14 selon l'espèce considérée) de plusieurs dizaines d'œufs (de 50 à 130) (**Fig. 2.3.A**). Entre chaque ponte, elles séjournent entre 10 et 30 jours en mer selon les espèces (**Fig. 2.3.B**). On appelle cette période l'intervalle inter-ponte (IP). Lors des voyages IP, les femelles se dispersent généralement en face des plages de ponte et peuvent parcourir plusieurs centaines de kilomètres.

Les études s'accordent sur le fait que, quand une femelle arrive sur son site de ponte, la vitellogénèse est achevée (Miller 1997) ; la femelle porte donc l'ensemble des follicules qui fournira le jaune des œufs qu'elle pondra dans la saison. Aussitôt qu'un follicule est ovulé, il entre dans l'oviducte où il sera fertilisé par le sperme d'un des mâles avec qui la femelle s'est accouplée (pontes polyandriques). Le développement de l'œuf commence immédiatement après la fertilisation. Le follicule fertilisé va continuer son parcours le long du tractus, où il va être au fur et à mesure enrobé d'albumen, puis entouré des membranes interne puis externe de la coquille. La coquille n'est que totalement formée environ sept jours après l'ovulation. Chaque ponte (jusqu'à l'avant-dernière) est suivie d'une ovulation, initiée par un pic d'hormones lutéinisantes et de progestérone (Owens 1997). Au cours de chaque intervalle inter-ponte a lieu le développement et la maturation (*i.e.* absorption d'eau) des œufs de la prochaine ponte.

A la fin de la saison de ponte, les femelles entament leur migration et rejoignent les zones d'alimentation distantes de plusieurs centaines à quelques milliers de kilomètres (**Fig. 2.3.C**). Selon les espèces, les zones d'alimentation peuvent être côtières et/ou océaniques. La durée de la migration varie selon les

espèces et les années, et dépasse généralement plusieurs années (**Fig.2.3.D**).

A chaque nouvelle saison de reproduction, les femelles retournent pondre sur la même plage (**Fig. 2.3.E**), ou groupe de plages, qui correspond également à la plage où elles sont nées (philopatrie, Miller 1997).

Les accouplements ont lieu aux abords des plages de ponte juste avant la saison de ponte (**Fig. 2.3.F**), après quoi les mâles retournent vers les zones d'alimentation (**Fig. 2.3.G**), alors que les femelles entament leur saison de ponte (**Fig. 2.3.A & B**).

Après 2 mois d'incubation dans le sable, les bébés tortues émergent du nid (**Fig. 2.3.H**). Les femelles ne reviennent pas s'occuper des petits, et le seul soin maternel consiste en la quantité d'énergie déposée dans le vitellus. Après être sortis du nid et avoir rejoint la mer, les bébés tortues entament une phase de « frénésie » de plusieurs jours, au cours desquels ils vont nager continuellement afin de rejoindre les zones océaniques (**Fig. 2.3.H**). Cette phase se repose uniquement sur l'apport énergétique du reste du vitellus que les bébés tortues ont absorbé à la fin du développement embryonnaire. Puis les petites tortues vont se laisser transporter par les courants océaniques et flotter parmi les amas d'algues en surface, où elles trouveront leurs premières sources alimentaires. Cette phase océanique, qui peut durer plusieurs années, est encore très peu connue, et est appelée « les années perdues (« *the lost years* », Carr 1952, **Fig. 2.3.I**).

Finalement, après une première phase de croissance et de développement, les jeunes tortues vont migrer vers les zones d'alimentation où elles achèveront leur croissance jusqu'au stade adulte, estimé être atteint entre 15 et 30 ans selon les espèces (Chaloupka & Musick 1997).

3. Méthodes et protocoles de suivi de la reproduction des tortues luth

3.1. Suivi historique de l'activité de ponte à Awala-Yalimapo

Les plages de l'ouest guyanais ont fait l'objet de comptages de pontes quasi-annuels depuis 1979 et d'un protocole d'identification individuel des femelles nidifiantes depuis 1985 par bagues métalliques Monel® ou Iconel®, et depuis 1995 par transpondeurs sous-cutanés (PIT, *Passive Integrative Transpondeur*, Trovan® ; Rivalan 2004, Fossette *et al.* 2008b), grâce au travail de bénévoles, d'ONG et de scientifiques. Bien que les efforts de suivi se soient focalisés sur la plage de Awala-Yalimapo, les protocoles non continus ou alternant les méthodes (méthode directe, par comptage des femelles ; méthode indirecte, par comptage des traces) et/ou la fréquence des patrouilles (quotidiennes, hebdomadaires) résultent en une base de données hétérogène (Rivalan 2004). Toutefois, ces suivis ont permis de retracer l'histoire de reproduction de la plupart des femelles (présence/absence par saison de reproduction) et d'établir des tendances de l'activité de ponte de la tortue luth (*e.g.* Fossette *et al.* 2008b, **Fig. 2.4**).

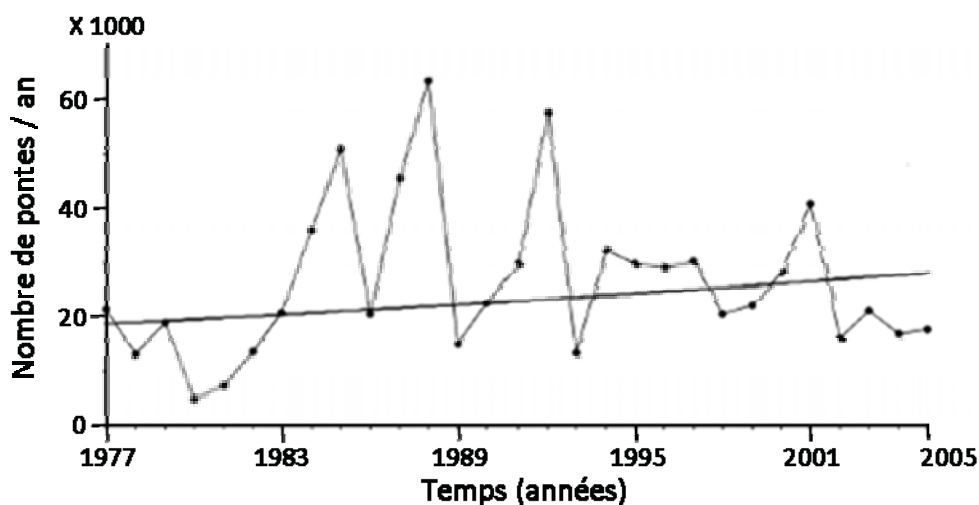


Figure 2.4. Tendence de l'activité de ponte des tortues luth en Guyane et au Suriname, issue d'un modèle basé sur les suivis réalisés de 1977 à 2005 (d'après Fossette *et al.* 2008b).

3.2. Suivi actuel de la population

Entre 2005 et 2011 (à l'exception de 2007), une équipe de l'IPHC a initié un suivi parallèle de la reproduction des tortues luth sur la plage de Awala-Yalimapo. Chaque année, de début mars à fin juillet, des patrouilles nocturnes quotidiennes ont été réalisées sur une portion de 4km de plage. Les tortues luth venant pondre majoritairement vers l'heure de marée haute (Chevalier & Girondot 1998), nous avons choisi de réaliser des patrouilles à partir de 4h avant jusqu'à 4h après chaque marée haute entre 18h et 8h, soit 8h minimum (voir l'exemple de calendrier de patrouilles **Boîte 2.2**). Chaque nuit, l'équipe de 6 patrouilleurs (minimum) se répartissait en trois groupes : 2 groupes de patrouille (1 moitié de plage/groupe) et un groupe relais. De cette manière, les patrouilles se déroulaient en continu, ce, jusqu'à la dernière tortue arrivée. Au cours des patrouilles, une lecture systématique de l'identité (PIT et bague) de chaque tortue luth rencontrée était réalisée. En plus du suivi classique de l'activité de ponte, 300 femelles choisies aléatoirement en 2005 et 2006 ont fait l'objet d'un suivi individuel biométrique, physiologique et de l'effort reproducteur tout au long de leur saison de reproduction. Dès qu'un patrouilleur identifiait une de ces femelles, le groupe relais allait à sa rencontre pour réaliser les manipulations (cf ci-dessous).

Ainsi nous avons pu réaliser le **suivi longitudinal** des femelles de cette sous-population sur une à trois saisons de reproduction successives en fonction des individus.

3.3. Suivi longitudinal

3.3.1. Performances reproductrices

- Nombre de pontes réalisées au cours de la saison

Basé sur les observations des pontes effectuées grâce au suivi quotidien des femelles nous avons calculé (*a posteriori*) le nombre de pontes que réalise chaque femelle au cours de sa saison de reproduction. Malgré notre protocole intensif de suivi de la population, il pouvait arriver qu'une ou plusieurs pontes n'ai(en)t pas été observée(s). Le calcul de l'ECF (*Estimated Clutch Frequency*) nous permet de faire une estimation aussi juste que possible du nombre total de pontes réalisées par chaque individu (Frazer & Richardson 1985, Rivalan *et al.* 2006). Le calcul de l'ECF consiste à prendre en compte les pontes non observées entre la première et la dernière ponte en se basant sur la durée moyenne d'un intervalle inter-ponte (10j, Girondot et Fretey 1996, Rivalan 2006; voir exemple **Fig. 2.5**).

Boîte 2.2. Extrait du calendrier de patrouilles de Mai 2009 (horaires de base).

Jour	Lune	HM1	Patrouille1 début	Patrouille1 fin	HM2	Patrouille2 début	Patrouille2 fin
ven	1	PQ	09:40 2,45m	05:30	08:00	23:38 2,33m	19:30 04:00
sam	2		11:28 2,37m				20:30 05:00
dim	3		00:41 2,42m			12:48 2,39m	21:30 06:00
lun	4		01:34 2,54m			13:48 2,46m	22:30 07:00
mar	5		02:20 2,65m			14:38 2,52m	23:00 08:00
mer	6		03:00 2,73m			15:21 2,55m	23:30 08:00
jeu	7		03:37 2,77m			15:59 2,54m	18:00 20:00
ven	8		04:12 2,79m	00:00	08:00	16:36 2,51m	18:00 20:30
sam	9	PL	04:45 2,78m	00:30	08:00	17:11 2,47m	18:00 21:00
dim	10		05:19 2,75m	01:00	08:00	17:47 2,41m	18:00 22:00
lun	11		05:52 2,70m	02:00	08:00	18:25 2,35m	18:00 22:30
mar	12		06:28 2,64m	02:30	08:00	19:06 2,28m	18:00 23:00
mer	13		07:08 2,56m	03:00	08:00	19:58 2,20m	18:00 23:59
jeu	14		07:53 2,45m	04:00	08:00	21:18 2,15m	18:00 01:30
ven	15		08:48 2,33m	05:00	08:00	22:35 2,14m	18:30 02:30
sam	16		09:56 2,23m	06:00	08:00	23:33 2,16m	19:30 03:30
dim	17	DQ	11:20 2,19m				20:30 04:30
lun	18		00:24 2,23m			12:31 2,23m	21:00 05:00
mar	19		01:10 2,34m			13:29 2,31m	21:30 06:00
mer	20		01:49 2,47m			14:19 2,42m	22:30 06:30
jeu	21		02:27 2,60m			15:04 2,52m	23:00 07:00
ven	22		03:05 2,74m			15:47 2,60m	18:00 20:00
sam	23		03:46 2,84m	00:00	08:00	16:30 2,64m	18:00 20:30
dim	24	NL	04:29 2,91m	00:30	08:00	17:15 2,65m	18:00 21:00
lun	25		05:15 2,93m	01:00	08:00	18:03 2,62m	18:00 22:00
mar	26		06:03 2,91m	02:00	08:00	18:56 2,58m	18:00 23:00
mer	27		06:54 2,86m	03:00	08:00	19:56 2,54m	18:00 23:59
jeu	28		07:49 2,77m	04:00	08:00	21:01 2,51m	18:00 01:00
ven	29		08:49 2,65m	05:00	08:00	22:06 2,49m	18:00 02:00
sam	30		09:57 2,51m	06:00	08:00	23:07 2,49m	18:00 03:00

Les phases de la lune (PQ, premier quartier ; PL, pleine lune ; DQ, dernier quartier et NL, nouvelle lune) ainsi que l'heure et la hauteur d'eau atteinte à marée haute (HM, Haute Mer) sont indiquées. Par exemple, la nuit du 7 au 8 mai, l'équipe a patrouillé la plage jeudi de 18h à 20h puis vendredi de minuit à 8h.

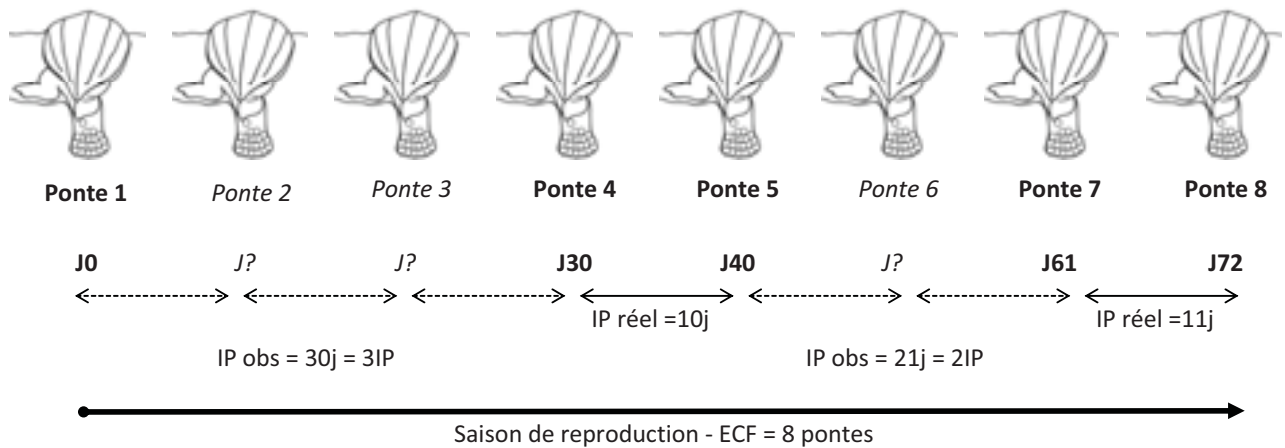


Figure 2.5. Schéma de la saison de reproduction d'une tortue luth hypothétique. L'individu a été observé pondre cinq fois au cours de sa saison de reproduction (en gras) sur 72 jours. A deux reprises la durée de l'intervalle inter-ponte (IP) observé était supérieure à la moyenne enregistrée au sein de notre population d'étude (10j). En se basant sur cette durée moyenne, nous pouvons estimer que trois pontes n'ont pas été observées (en italique). Ainsi, l'ECF calculé est de 8 : l'individu a réalisé 8 pontes pendant sa saison de reproduction.

- Taille de la ponte

Après être montée sur la plage et avoir commencé à installer sa zone de ponte (balayage du sable sur la zone choisie), chaque femelle était surveillée par un expérimentateur. Dès le début de la ponte, l'expérimentateur comptait le nombre d'œufs fertiles pondus à l'aide d'un compteur à main. Ce comptage était effectué à chaque ponte observée de chacune des femelles, dans la mesure du possible. En effet, il pouvait arriver que plusieurs femelles de notre sous-population arrivent sur la plage au même moment, et selon leur répartition sur la plage, l'équipe ne pouvait réaliser les manipulations sur chacune d'entre elles. En 2005 et 2006, la première ponte de chaque femelle était pesée, et 3 œufs étaient prélevés à chaque ponte et individuellement pesés afin d'estimer la masse des pontes ultérieures (**Fig. 2.6**; voir détails dans **Article 2**).

3.3.2. Caractéristiques morphologiques des femelles

Le suivi biométrique que nous avons réalisé consistait à mesurer la longueur, la largeur, la circonférence et la masse corporelle de chaque femelle de notre sous-population, suivant la méthode détaillée par Georges & Fossette (2006). Brièvement, pendant la ponte, la longueur

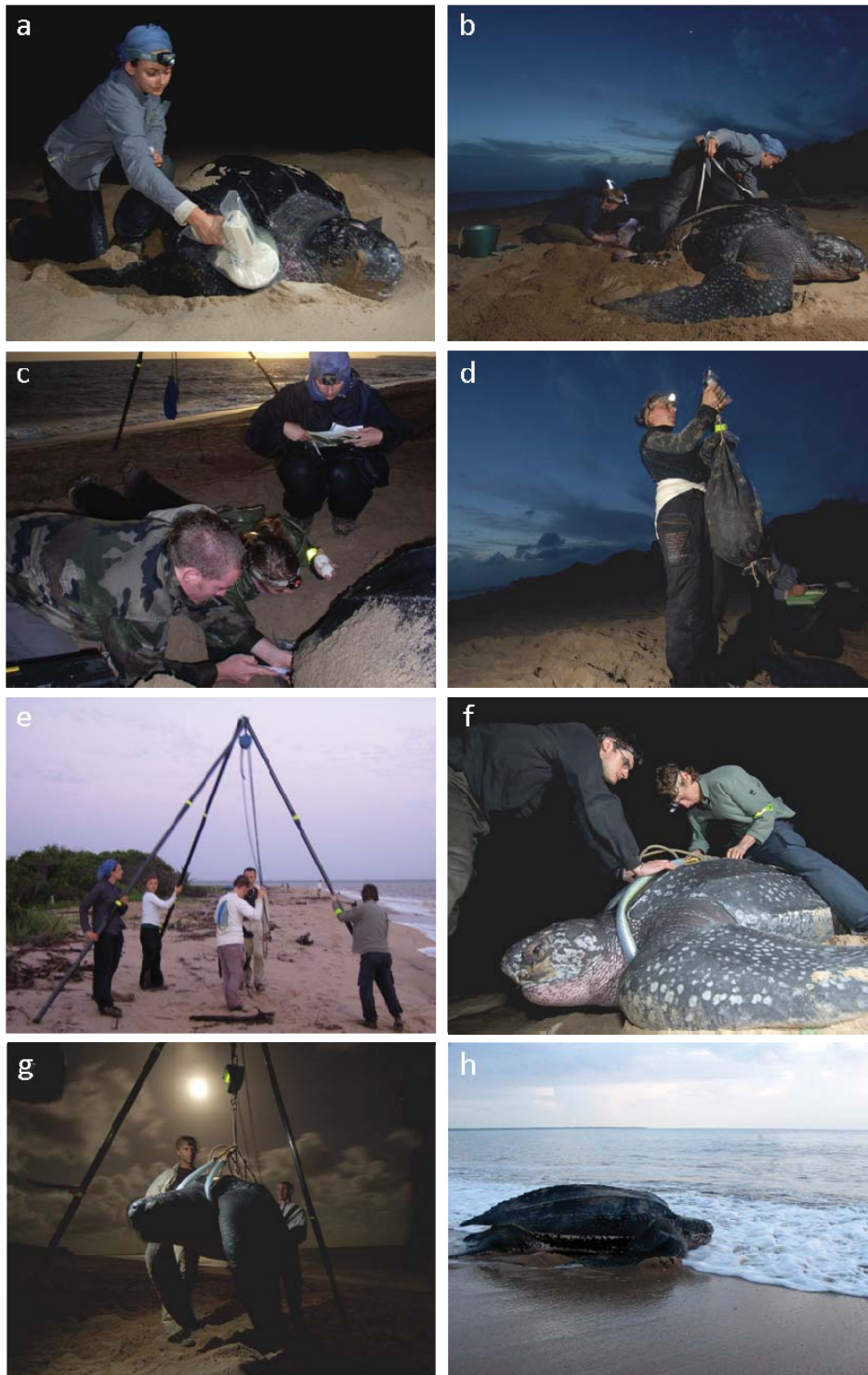


Figure 2.6. Protocole du suivi longitudinal des tortues luth mis en place pour cette étude : (a) Vérification de l'identité de la tortue par lecture de son transpondeur ; (b) Pendant la ponte, mesure de la longueur et de la largeur de carapace, comptage des œufs, (c) prélèvement d'œufs et prise de sang ; (d) A la fin de la ponte, pesée des œufs ; (e-g) Pesée de la tortue : (e) installation du trépied où est suspendu le palan et le peson, (f) mise en place du harnais, (g) mesure de la circonférence et lecture de la masse lorsque que la tortue est soulevée ; (h) départ à la mer de la tortue. (© S Unterthiner (a-b, d, f-g), L Gagnon et VP).

(d'une extrémité à l'autre de la crête médiane) et la largeur (au plus large, derrière les épaules) de la dossière étaient mesurées à l'aide d'un ruban souple. Après la ponte, lorsque la tortue se dirigeait vers la mer pour repartir, un harnais était placé devant elle, mis en place et fermé au fur et à mesure de ses déplacements. Enfin, la tortue était soulevée grâce à un palan à chaîne suspendu à un trépied de 4,5 m de haut et auquel était attaché un peson (600 kg, Kern, Germany). Alors, la circonférence pouvait être mesurée, et la lecture de la masse effectuée (**Fig. 2.6**).

Entre deux saisons de reproduction, *i.e.* pendant leur migration, les tortues luth nidifiant en Guyane se dispersent dans l'Atlantique nord à la recherche de nourriture (Ferraroli *et al.* 2004, Fossette *et al.* 2010a, **Annexe 1**). Grâce à une collaboration avec une équipe de recherche canadienne (menée par MC James, Université de Dalhousie) nous avons eu accès aux paramètres biométriques (longueur, largeur de carapace et circonférence) de 29 femelles tortues luth capturées sur leur site d'alimentation en Nouvelle Ecosse, Canada.

3.3.3. Caractéristiques physiologiques des femelles

Un prélèvement sanguin (8mL) systématique a été réalisé sur chaque tortue observée pendant la ponte (**Fig. 2.6**) pour réaliser le suivi des paramètres physiologiques. Pour 35 individus venus se reproduire en 2006 et prélevés régulièrement tout au long de leur saison de ponte, les concentrations plasmatiques de glucose, des triglycérides, de l'urée et de calcium ont été mesurées et l'hématocrite a été déterminé. Les concentrations des métabolites et du calcium ont été mesurées par colorimétrie enzymatique grâce à des kits commerciaux (glucose: Glucose-RTU, 61 269/61 270; triglycérides: TG-PAP 150, 61 236; urée: Urea-Kit S180, 61 912/61 913, BioMérieux et Calcium : Ca-Kit 61041, Thermo Fischer Scientific).

3.3.4. Indice moléculaire : les télomères

Nous avons choisi d'utiliser les télomères comme indice des coûts de la reproduction, car comme nous l'avons vu dans l'introduction, ils induisent un raccourcissement des télomères via le stress oxydatif. Par ailleurs, nous avons testé la pertinence des télomères comme indice de la qualité reproductrice individuelle des tortues luth.

Les télomères étant présents dans toutes les cellules d'un organisme, leur longueur peut se mesurer sur divers types de tissus. Toutefois, la longueur des télomères reste le plus souvent mesurée dans des échantillons de cellules sanguines. Chez les tortues marines, les érythrocytes sont nucléés, ce qui facilite l'extraction de l'ADN.

Dans un premier temps, l'extraction de l'ADN a été réalisée en utilisant les kits commerciaux DNeasy Blood and Tissue Kit (QIAGEN). Puis, nous avons réalisé la mesure de la longueur des télomères grâce à la technique de réaction en chaîne par polymérase quantitative (qPCR), selon la procédure détaillée par Criscuolo *et al.* (2009), que nous avons adaptée aux tortues marines (voir **Article 4**).

3.4. Caractéristiques environnementales

Afin de caractériser les conditions environnementales rencontrées par les tortues luth lors de leurs migrations, nous avons utilisé l'indice d'oscillation Nord Atlantique (indice NAO). L'indice NAO représente l'alternance nord-sud de la circulation atmosphérique de la région de l'Atlantique Nord et est considéré comme l'indice le plus robuste impliqué dans les systèmes atmosphériques et climatiques de cette région. L'indice NAO alterne entre des phases positive et négative associées à des variations de la direction et de la vitesse des vents qui induisent des changements des températures et des précipitations. Il a été montré que l'indice NAO influence de manière considérable les systèmes écologiques (Stenseth *et al.* 2003) et notamment les variations de distribution et d'abondance des ressources trophiques des océans, dont les planctons gélatineux (Attrill *et al.* 2007). Bien que l'indice NAO présente des variations tout au long de l'année, celles-ci sont d'une amplitude plus importante pendant les mois d'hiver (de décembre à mars). C'est la raison pour laquelle l'indice NAO utilisé pour étudier l'effet des conditions environnementales sur les systèmes écologiques est communément calculé pendant les mois d'hiver (*e.g.* Stenseth *et al.* 2003, Attrill *et al.* 2007).

3. RESULTATS PRINCIPAUX



1. Gestion des réserves corporelles chez la tortue luth

Par définition (Drent & Dan 1980), les reproducteurs sur capital stockent la totalité des réserves corporelles destinées à leur reproduction. Dans le cadre de notre hypothèse selon laquelle les tortues luth seraient des reproducteurs sur capital, on s'attend à ce que les femelles reproductrices présentent une capacité importante de stockage des réserves corporelles en anticipation de leur reproduction. Ceci devrait s'illustrer par des différences contrastées dans les caractéristiques morphologiques entre les périodes d'alimentation et de reproduction. De plus, les coûts métaboliques n'étant assurés, au cours de la reproduction, que par l'utilisation des réserves corporelles, on s'attend à une variation des paramètres morphologiques et physiologiques au cours de la saison de ponte caractéristique d'une période de jeûne.

1.1. Capacités morphologiques de stockage des réserves corporelles

En comparant des indices biométriques (circonférence et longueur de carapace) de femelles tortues luth adultes sur un de leurs sites de reproduction en Guyane et sur un de leurs sites d'alimentation au large de la Nouvelle-Ecosse, nous montrons (**Article 1**) que les tortues luth ont un rapport circonférence/longueur de carapace significativement plus élevé sur le site d'alimentation que sur le site de reproduction (**Fig. 3.1**).

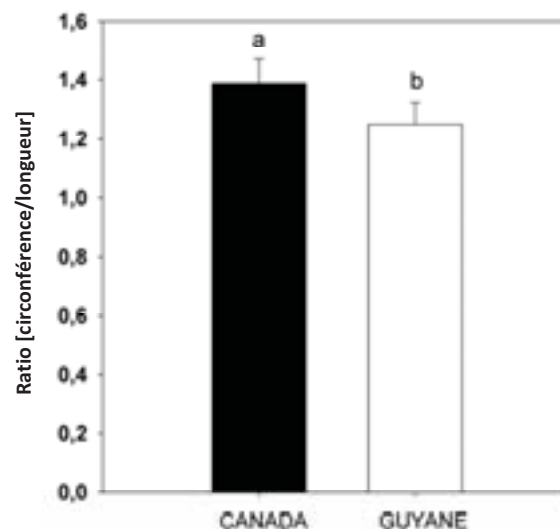


Figure 3.1. Comparaison du ratio [circonférence/longueur de carapace] des tortues luth sur site d'alimentation en Nouvelle-Ecosse, Canada (n = 29) et sur site de reproduction en Guyane (n = 182). Les lettres indiquent une différence significative (Article 1).

Ce suivi transversal indique que pour une longueur donnée, les femelles luth sont plus grosses sur leur site d'alimentation que sur leur site de reproduction. Ainsi, en utilisant la relation existant entre la masse corporelle, la longueur et la circonférence (Georges & Fossette 2006), nos résultats indiquent que pour une tortue d'une longueur moyenne de carapace de 160 cm, sa masse corporelle serait de 477 kg sur site d'alimentation et de 395 kg sur site de reproduction, soit une différence de l'ordre de 80 kg.

Par ailleurs, sur le site d'alimentation, le rapport [circonférence/longueur de carapace] augmente de 17% en 100 jours (**Fig. 3.2**). Toujours en se basant sur la relation de Georges & Fossette (2006) chez une tortue moyenne de 160 cm, l'amplitude de cette augmentation correspondrait à un gain de 112 kg, soit environ 1kg/jour de résidence sur site d'alimentation. Ces calculs sont à titre indicatif, puisqu'il ne s'agit pas des mêmes tortues mesurées au cours de la période d'alimentation.

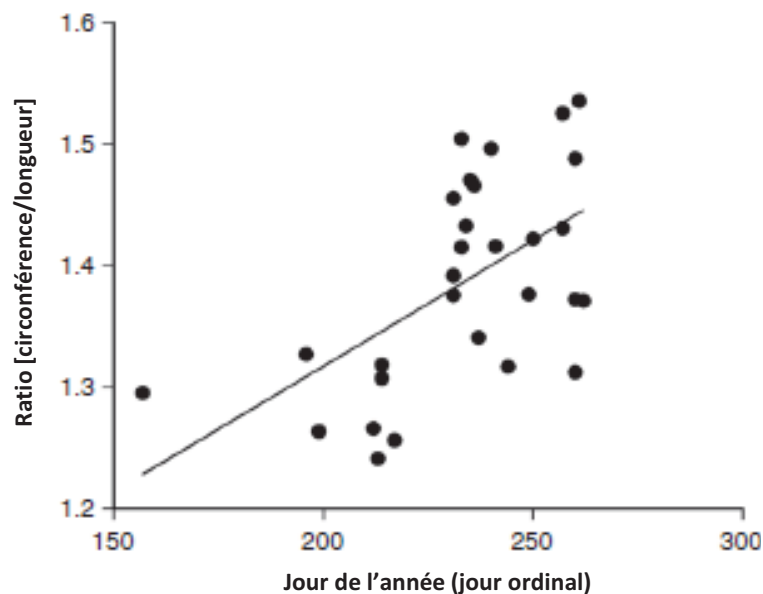


Figure 3.2. Variation du ratio [circonférence/longueur de carapace] en fonction du jour de capture des tortues luth mesurées (n = 29) sur leur zone d'alimentation dans les eaux de Nouvelle-Ecosse, Canada (Article 1). Cette figure illustre la prise d'embonpoint des tortues luth sur les sites d'alimentation.

Des autopsies de tortues luth capturées sur site d'alimentation (Davenport *et al.* 1990) ont révélé l'existence d'importantes quantités de tissus adipeux sous la dossière et sous le plastron. L'augmentation du ratio [circonférence/longueur de carapace] sur le site d'alimentation pourrait donc refléter le stockage des réserves corporelles sous forme de tissus adipeux sous la dossière des tortues luth.

L'ensemble de ces résultats témoigne de la capacité importante de stockage des réserves corporelles lipidiques chez la tortue luth. Celle-ci peut- être associée à la structure particulière de leur carapace non rigide (Wynecken 2001), comme illustré par la **Fig. 3.3** présentant une même femelle photographiée au Canada et en Guyane.



Figure 3.3. Tortue luth (n° 0126-268B) observée en Avril 2009 sur le site de reproduction en Guyane (en haut, VP) puis capturée en Juillet 2010 sur le site d'alimentation au Canada (en bas, © Canadian Sea Turtle Network, MC James). Cette figure illustre les capacités de stockage des tortues luth, comme le révèle la forme rebondie du cou, de la carapace et des épaules sur le site d'alimentation qui contraste avec l'absence de « bourrelets » au cou et le creusement de la carapace entre les carènes sur le site de ponte.

1.2. Stratégies d'utilisation des réserves corporelles pendant la reproduction

1.2.1. Approche biométrique

Grâce à un suivi longitudinal unique de la biométrie de 35 tortues luth tout au long de leur saison de ponte en Guyane, nous montrons (**Article 2**) qu'au début de la saison de ponte, les femelles mesurent en moyenne $159,0 \pm 1,5$ cm de long, $116,0 \pm 1,0$ cm de large pour une masse corporelle de $409,0 \pm 8,9$ kg, correspondant à un indice de condition corporelle de $25,1 \pm 1,8$. Au cours de leur saison de ponte qui dure en moyenne $71,2 \pm 2,6$ jours, les femelles perdent significativement de la masse de manière non linéaire : jusqu'à la moitié de la saison de ponte, la perte de masse varie entre 10 et 5 kg entre deux pontes successives espacées en moyenne de 10 jours, avant de se stabiliser à ~ 5 kg entre deux pontes successives jusqu'à la fin de la saison de ponte. Ainsi, au cours de leur saison de ponte, les femelles perdent en moyenne $46,8 \pm 2,6$ kg (masse finale moyenne : $364,7 \pm 7,4$ kg) soit 11% de leur masse en début de saison. L'indice de condition corporelle diminue également au cours de la saison de ponte, mais de manière linéaire, devenant négatif à la moitié de la saison de ponte et égal à $-20,6 \pm 1,1$ en fin de saison. De plus, nous montrons qu'il existe un seuil de condition corporelle en début de saison (~ 18) en deçà duquel les femelles altèrent considérablement leur condition pendant la saison de ponte (**Fig. 3.4**). Ceci suggère l'existence d'un seuil minimum de condition requis au préalable pour l'engagement dans la reproduction.

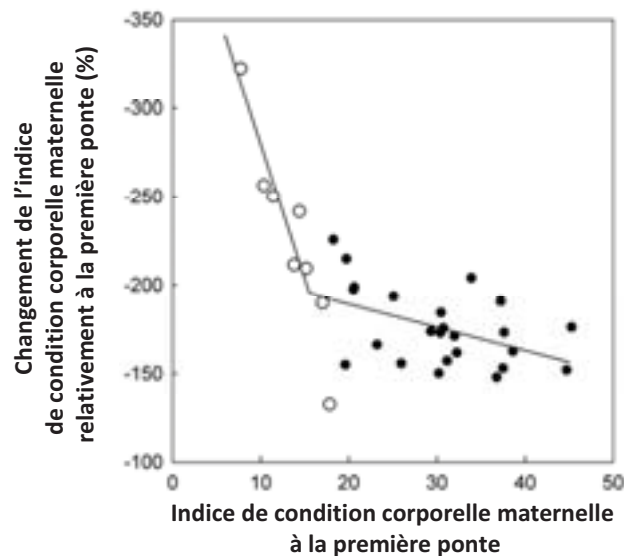


Figure 3.4. Relation entre le changement d'indice de condition corporelle des femelles au cours de la saison de reproduction et leur indice de condition corporelle à la première ponte. Cette figure illustre l'existence d'un seuil de condition corporelle en début de saison de ponte en deçà duquel les femelles altèrent considérablement leur condition (en blanc).

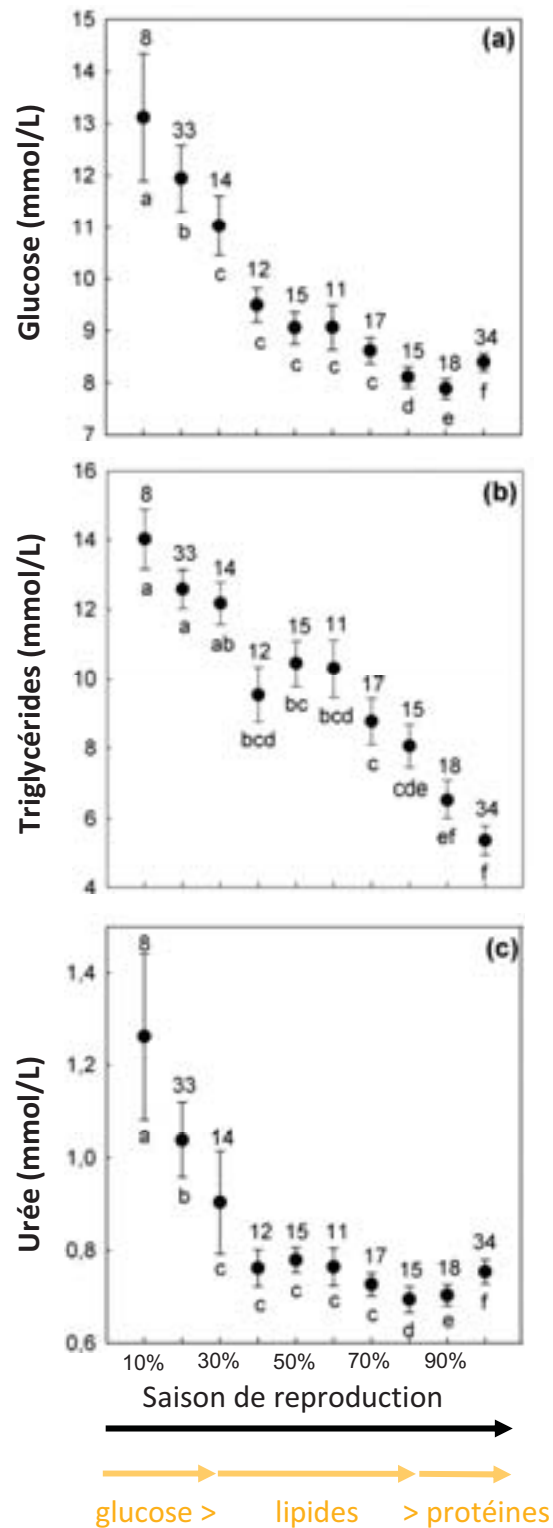


Figure 3.5. Variation des concentrations plasmatiques de glucose (a), triglycérides (b) et urée (c) chez 35 femelles tortue luth au cours de la saison de ponte. Les chiffres indiquent le nombre d'individus, et les lettres, les différences significatives. Cette figure illustre la mobilisation séquentielle des différents substrats énergétiques des réserves corporelles comme indiqué en orange (Article 2).

1.2.2. Approche physiologique

En parallèle à ce suivi biométrique, plusieurs paramètres plasmatiques ont été mesurés sur ces mêmes 35 femelles. Nous montrons (**Article 2**) que les concentrations plasmatiques de glucose, triglycérides et urée, indicatrices respectivement d'un métabolisme glucidique, lipidique et protéique, présentent une forte variabilité inter-individuelle en début de saison de ponte (**Tableau 3.1**). Cette variabilité prononcée indique que les femelles seraient dans un état nutritionnel différent, et au regard du glucose, que certaines femelles commenceraient leur saison de ponte dans un état post-absorptif.

Métabolites	Moyenne \pm SE [min ;max] (mmol.L ⁻¹)
Glucose	12,46 \pm 0,64 [8,66 ; 24,00]
Triglycérides	12,89 \pm 0,56 [2,10 ; 19,60]
Urée	1,14 \pm 0,08 [0,33 ; 2,13]

Tableau 3.1. Concentrations plasmatiques des métabolites mesurées à la première ponte des 35 femelles suivies.

Par la suite, la saison de ponte est caractérisée par une diminution significative de tous les paramètres physiologiques chez tous les individus (**Fig. 3.5**). D'une part, les niveaux de glucose et d'urée diminuent pendant le premier tiers de la saison, jusqu'à atteindre un seuil minimal au deuxième tiers de la saison, avant d'augmenter légèrement à la fin du dernier tiers de la saison de ponte (**Fig. 3.5.a&c**). D'autre part, les concentrations de triglycérides diminuent de manière linéaire tout au long de la saison (**Fig. 3.5.b**).

La cinétique de ces paramètres plasmatiques chez les femelles luth pendant la reproduction est semblable à celle décrite chez des animaux au cours d'une longue période de restriction alimentaire (*e.g.* Robin *et al.* 1998, Jenni-Eiermann & Jenni 1998, McCue 2007) et reflète la mobilisation séquentielle des différents substrats énergétiques des réserves corporelles que sont les glucides, les lipides, puis les protéines. Par ailleurs, la diminution linéaire des triglycérides suggère qu'au cours de la saison de ponte, les femelles comptent essentiellement sur leurs réserves lipidiques. Ces résultats concordent avec ceux de l'**Article 1** illustrant le mode de stockage des réserves corporelle des tortues luth.

En fin de saison, les faibles différences inter-individuelles en triglycérides et la légère augmentation des concentrations d'urée (**Fig. 3.5.b & c**) suggèrent un possible changement de voie métabolique des lipides vers les protéines (**Fig. 3.5**). Ce changement métabolique est identique à celui décrit chez les animaux à la fin d'un jeûne prolongé (*e.g.* oiseaux : Robin *et al.* 1998, mammifères : Cherel *et al.* 1992, reptiles : McCue 2007).

D'autre part, les concentrations plasmatiques de calcium ont diminué de manière linéaire tout au long de la saison de ponte (**Article 2**), suggérant une diminution progressive des réserves maternelles en calcium au cours de la reproduction. Ainsi, les réserves de calcium des femelles pourraient être un facteur limitant leur performance de reproduction.

L'ensemble de ces résultats, basés sur des approches biométrique et physiologique des caractéristiques maternelles et des stratégies de gestion des réserves corporelles, soutient l'hypothèse selon laquelle les tortues luth de Guyane opèrent comme des reproducteurs sur capital.

En 2009, nous avons procédé à l'extraction de 2,6 kg de déchets de matière plastique chez une femelle présentant des difficultés à pondre au cours de la 3^{ème} ponte de sa saison (**Article 3**). Si cette anecdote de terrain illustre le fait que les tortues marines sont directement affectées par la pollution marine, elle illustre également le fait que les tortues pourraient chercher à se nourrir pendant leur saison de ponte. En effet, il a été rapporté que les tortues luth pouvaient confondre les sacs plastiques flottants avec leurs proies principales, les méduses (Mrosovsky 1981). Si la durée du transit intestinal décrite chez la tortue caouanne (9 jours, Valente *et al.* 2008) s'applique aux tortues luth, cette observation tendrait à suggérer que cette tortue aurait ingéré ces déchets pendant sa saison de ponte par confusion avec des méduses. Toutefois, compte tenu du faible contenu énergétique des méduses (Doyle *et al.* 2007), une prospection alimentaire active au cours de la saison de ponte s'avérerait être une stratégie inefficace en terme énergétique, comme l'indiquent nos résultats biométrique et physiologique (**Article 2**).

2. Effort reproducteur des tortues luth

Comme toutes les tortues marines, les tortues luth présentent une absence de soins parentaux post-nataux (Miller 1997). La totalité des ressources maternelles allouée dans leur reproduction est donc directement liée à la performance reproductrice (*i.e.* nombre d'œufs pondus sur une saison) réalisée dans la saison de ponte (Clutton-Brock 1991). Compte tenu de l'importante capacité de stockage des réserves corporelles des tortues luth (**Article 1**), on peut donc s'attendre d'une part, à ce que les femelles réalisent une performance reproductrice importante et d'autre part, à ce que la condition corporelle des femelles au début de la saison de ponte influe sur leur qualité reproductrice.

2.1. Performance reproductrice à l'échelle d'une saison

En parallèle aux suivis biométrique et physiologique des 35 femelles, le suivi individuel de leurs performances reproductrices a été réalisé. Nous montrons (**Article 2**) qu'au cours d'une saison de ponte, les tortues luth réalisent en moyenne $8,3 \pm 0,3$ pontes (entre 5 et 12 pontes) de $86,9 \pm 2,2$ œufs ($7,2 \pm 0,2$ kg d'œufs) chacune, soit un nombre total moyen de 717 ± 28 œufs représentant une masse de $59,7 \pm 2,4$ kg. La taille et la masse des pontes ne varient pas au cours de la saison de ponte. La production moyenne d'œufs sur une saison de ponte équivaut ainsi à 15% de la masse corporelle moyenne des femelles en début de saison. Ces résultats illustrent les coûts élevés liés à la reproduction à l'échelle d'une saison de ponte (cf. **Article 4**) et reflètent l'importance de la condition corporelle maternelle seuil.

En effet, nous montrons que l'effort reproducteur (exprimé en nombre de pontes ou en nombre total d'œufs pondus sur une saison) est plus élevé chez les femelles en meilleure condition en début de saison de ponte (**Fig. 3.6**).

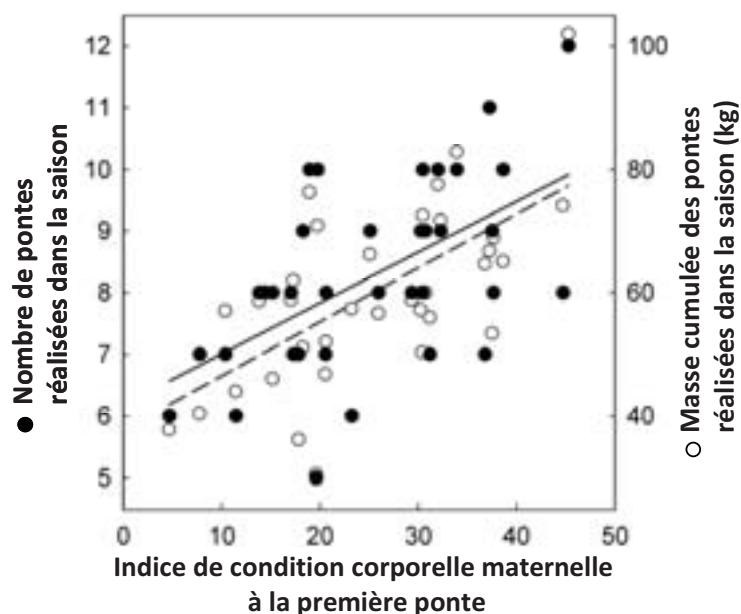


Figure 3.6. Relation entre la condition corporelle maternelle en début de saison de reproduction et la performance de reproduction sur une saison. Cette figure illustre l'importance de la condition corporelle dans la reproduction de la tortue luth.

Par ailleurs, il est intéressant de remarquer que la perte de masse totale des femelles est en moyenne 13 kg inférieure à la masse cumulée des pontes. Cette différence pourrait s'expliquer par une ingestion d'eau au cours de la saison, permettant d'assurer la maturation des œufs constitués à 67% d'eau chez la tortue luth (Wallace *et al.* 2006).

2.2. Indice de la qualité reproductrice à l'échelle d'une saison

Si la condition des tortues luth en début de saison de ponte constitue un bon indicateur de leur qualité reproductrice individuelle (ci-dessus, **Article 2**), nous montrons par ailleurs (**Article 4**) que la performance de reproduction d'une saison est plus fortement corrélée à la taille des télomères mesurés dans les érythrocytes maternels qu'à leur condition ou à la longueur de leur carapace. Chez les oiseaux, la variabilité inter-individuelle de la longueur et de l'attrition des télomères est positivement reliée à certaines composantes de la valeur sélective (*e.g.* Bize *et al.* 2009) et notamment au succès reproducteur au cours de la vie (Pauliny *et al.* 2006). Toutefois, aucune étude ne s'était jusqu'à présent intéressée à ces questions chez les tortues marines. Ainsi, nous proposons que la longueur des télomères constitue un nouvel indicateur de la qualité reproductrice individuelle chez les tortues luth.

3. Liens entre migration et reproduction

La migration des tortues marines est la période pendant laquelle les femelles constituent les réserves corporelles destinées à leur prochaine reproduction (Miller 1997, **Article 1**). On peut donc s'attendre à ce que la qualité reproductrice et la condition des femelles lors d'une saison de ponte donnée dépendent de la période de migration précédente.

3.1. A l'échelle d'un cycle de reproduction

Nous montrons (**Article 4**) que les femelles ayant des télomères plus courts sont celles ayant effectué une migration plus courte (*i.e.* 2 ans *vs* 3 ans ; **Fig. 3.7**). L'attrition des télomères étant induite par le stress oxydatif causé par le métabolisme (Von Zglinicki 2002), nous proposons qu'une migration de 2 ans, donc une restauration des réserves plus rapide, pourrait induire des coûts métaboliques plus élevés, résultant en des télomères plus courts. Par ailleurs, les femelles revenant d'une migration de 2 ans ont moins pondu en moyenne que celles revenant d'une migration de 3 ans (**Fig. 3.7**). Ces résultats indiquent qu'il est plus coûteux, en terme de stockage des ressources, et moins efficace, en terme de performance reproductrice, de se reproduire après une migration de 2 ans qu'après une migration de 3 ans.

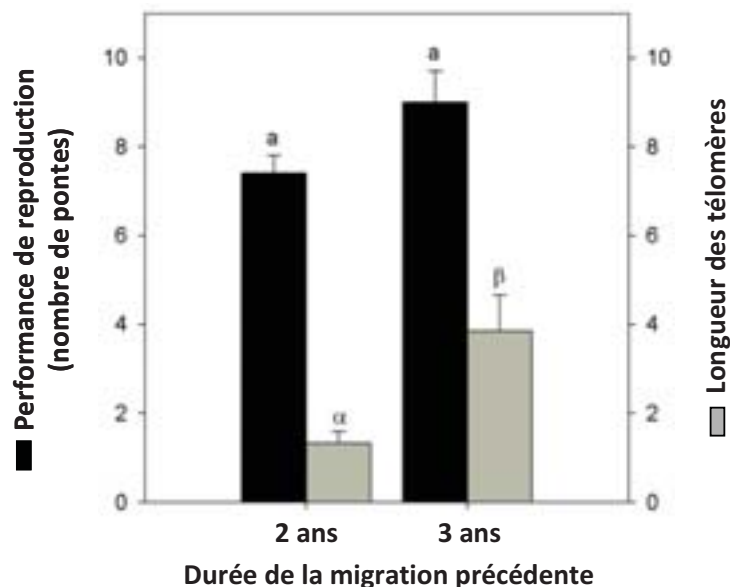


Figure 3.7. Performance reproductrice (nombre de pontes) et longueur des télomères (T/C ratio) chez des tortues luth ($n = 22$) au cours d'une saison de reproduction (2005 ou 2006) en relation avec la durée de la migration précédant la saison de ponte. Les lettres indiquent les différences significatives. Cette figure illustre à l'échelle d'une saison les compromis entre le stockage des ressources au cours de la migration et l'effort reproducteur pendant la saison suivante (**Article 4**).

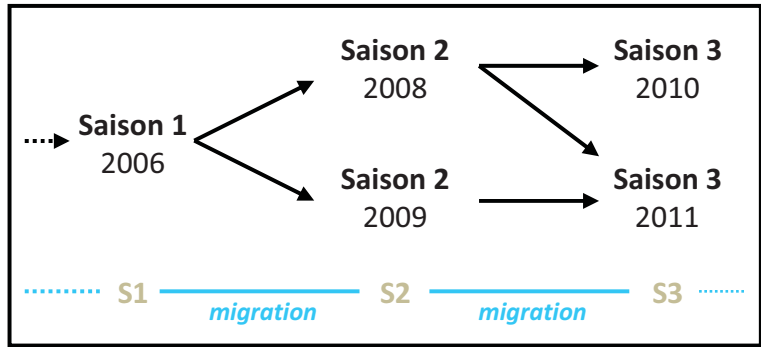


Figure 3.8. Schématisation du suivi longitudinal des 27 femelles tortues luth, au cours de leurs reproductions successives, de 2006 à 2011.

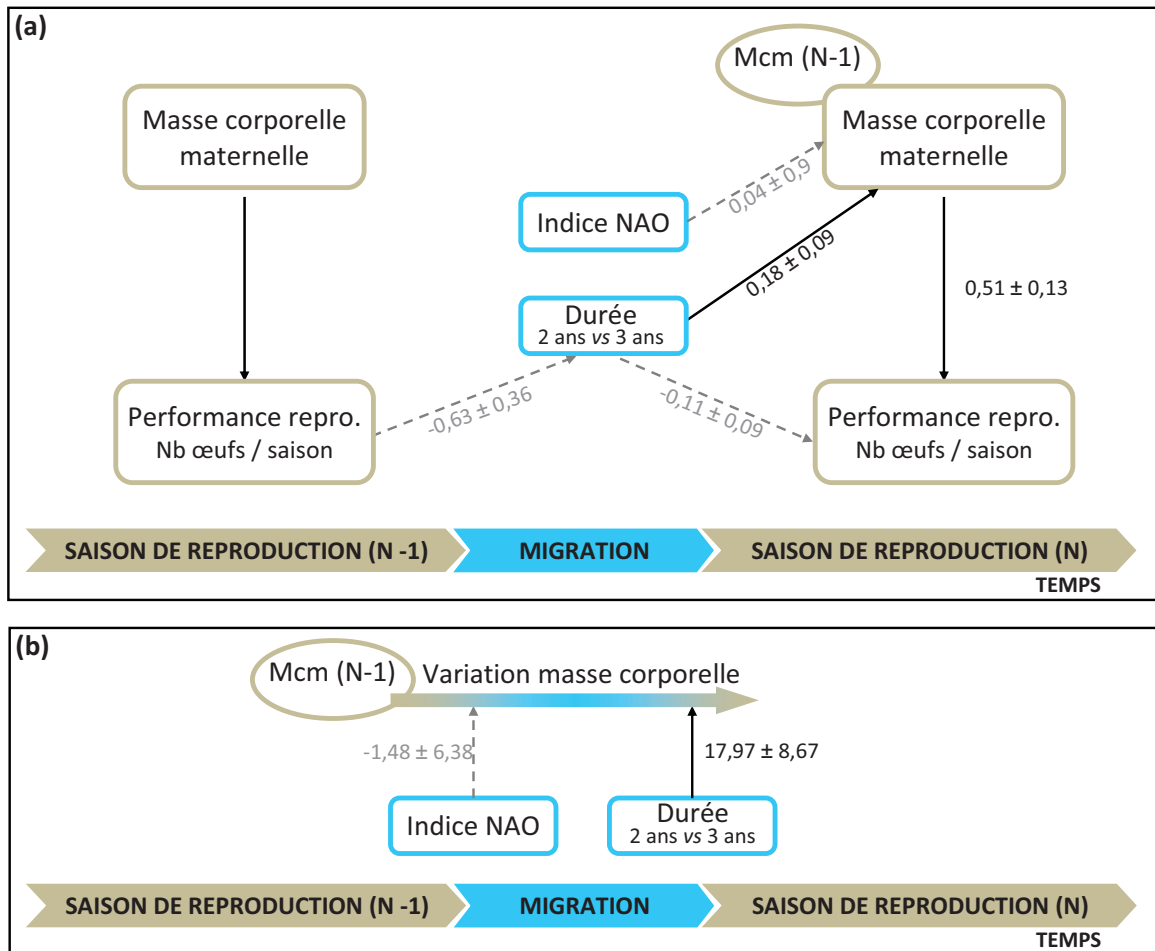


Figure 3.9. Schéma général des liens entre migrations (bleu) et reproduction (beige) chez 27 femelles tortues luth suivies au cours de leurs reproductions successives de 2006 à 2011. Les flèches noires et pleines indiquent une relation significative, alors que les flèches grises en pointillés indiquent une relation non significative. Les chiffres associés aux flèches correspondent aux coefficients des relations (± 1 SD). L'indice d'oscillation Nord Atlantique (NAO) est calculé à partir des indices mensuels, voir Partie 2). Le paramètre Mcm (N-1), *i.e.* masse corporelle maternelle de la saison précédente, est placée dans un ovale lorsqu'elle est considérée en covariable (voir Annexe 2 pour les méthodes).

Par ailleurs, il est intéressant de remarquer qu'en Guyane les femelles tortue luth réalisent majoritairement (*i.e.* 75%) des migrations de 2 ans (Rivalan *et al.* 2005). Cette proportion plus élevée d'un mode de migration apparemment plus coûteux et moins efficace à l'échelle d'une saison (notre étude) est paradoxal et suggère l'existence de compromis associé à la reproduction.

3.2. A l'échelle de plusieurs cycles de reproduction successifs (résultats préliminaires)

Afin de mieux comprendre les compromis associés à la reproduction des tortues luth de Guyane (**Article 4**), il est nécessaire de travailler sur une échelle de temps intégrant plusieurs cycles de reproduction. Nous nous sommes donc basés sur le suivi longitudinal de 27 femelles sur 3 saisons de pontes successives de 2006 à 2011 (**Fig. 3.8**).

3.2.1. Généralisation des résultats obtenus à l'échelle d'un cycle de reproduction

Nous montrons, d'une part, quelle que soit l'année considérée, que la réalisation d'une migration plus longue (3 ans) est plus profitable pour les femelles en terme de masse corporelle (**Fig. 3.9.a**). En effet, les femelles qui ont réalisé une migration de 3 ans présentent un gain de masse de 18 kg supérieur à celui de celles qui ont réalisé une migration de 2 ans (**Fig. 3.9.b**). D'autre part, à chaque saison de ponte, la performance reproductrice des femelles ne dépend pas de la durée de la migration précédente ; par contre, elle est positivement reliée à la masse corporelle au début de la saison de ponte (**Fig. 3.9.a**). De plus, nous montrons que la performance reproductrice d'une saison n'est pas reliée à la durée de la migration qui suit (**Fig. 3.9.a**). Ceci suggère, qu'indépendamment de sa durée, la migration entre deux saisons de reproduction suffit à restaurer les réserves maternelles et à franchir le seuil minimum de condition nécessaire pour s'engager dans la reproduction suivante (cf. **Article 2**). Compte tenu qu'un surplus d'énergie investi dans la reproduction est positivement corrélé à la performance de reproduction (Smith & Fretwell 1974, Bonnet *et al.* 2001), et qu'une migration de 2 ans suffirait à atteindre le seuil minimal de réserves corporelles, le surplus de réserves acquis lors d'une année supplémentaire de migration (*i.e.* migration de 3 ans) permettrait donc aux femelles de réaliser une meilleure performance de reproduction. L'important effort reproducteur réalisé par les tortues luth au cours d'une saison (**Article 2**)

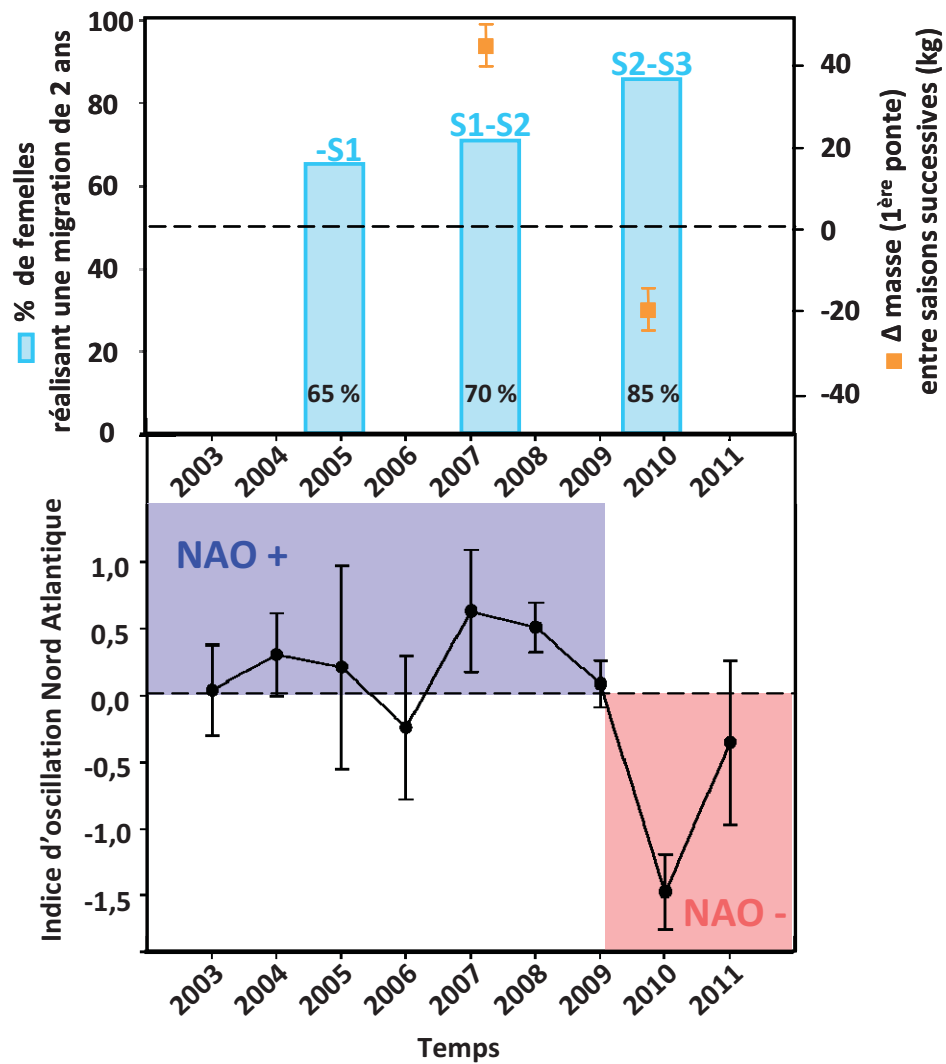


Figure 3.10. Variation des caractéristiques maternelles et environnementales au cours de 3 cycles de reproduction successifs, tenant compte des 3 saisons de ponte (S1, S2 et S3) considérées dans notre suivi longitudinal. En haut, sont représentées la proportion des femelles ayant réalisé une migration de 2 ans (bleu turquoise) et la variation de la masse corporelle maternelle en début de saison entre saisons successives (orange). En bas, figure la variation de l'indice d'oscillation Nord Atlantique (NAO, calculé de l'hiver 2002-2003 à l'hiver 2010-2011 à partir des indices mensuels, voir Partie 2). Notez l'alternance d'une phase positive (en bleu indigo) jusqu'à la saison de ponte 2009, suivie d'une phase négative (rouge).

et les coûts associés aux migrations plus courtes (**Article 4**) devraient amener les femelles à différer la saison de ponte suivante, donc à réaliser des migrations de 3 ans (*reproductive skipping strategy*, Bull & Shine 1980, Clutton-Brock 1998). Paradoxalement, sur toute la durée du suivi, les femelles ont majoritairement effectué des migrations de 2 ans (73,5%), en accord avec les études précédentes (Rivalan *et al.* 2005). On peut penser, comme le proposait Rivalan *et al.* (2005), que les femelles qui se reproduisent tous les 2 ans, *i.e.* plus fréquemment, auraient au terme de leur vie, un succès reproducteur plus important.

3.2.2. Variation des caractéristiques maternelles et environnementales au cours de 3 cycles de reproduction successifs

Au cours de notre suivi, la proportion de femelles réalisant des migrations de 2 ans était variable: sur les trois cycles considérés, 65%, 70,4% et 85,2% des femelles ont réalisé des migrations de 2 ans (**Fig. 3.10**), ce qui suggère qu'au cours de leur vie reproductrice les femelles ajustent la durée de leur migration. De plus, notre suivi montre une variabilité intersaison marquée de la masse corporelle des femelles : entre la saison 1 et la saison 2, les femelles ont pris en moyenne $44,3 \pm 4,9$ kg (soit $+19,2 \pm 1,9$ kg/an), alors qu'entre la saison 2 et la saison 3, elles ont perdu en moyenne de $19,2 \pm 5,3$ kg (soit $-9,3 \pm 2,6$ kg/an). Ainsi, la période au cours de laquelle une plus grande proportion de femelles a réalisé une migration de 2 ans correspond à la période la moins profitable pour les femelles, en termes de capitalisation des réserves corporelles. On peut supposer que l'ajustement de la durée des migrations au cours du temps serait dû à une variation des conditions environnementales. A l'échelle de l'océan Atlantique, il est admis que l'alternance des phases positives et négatives de l'indice d'oscillation Nord Atlantique (NAO) a un impact sur l'abondance des ressources trophiques océaniques (*e.g.* Parsons & Lear 2001, Stenseth *et al.* 2003, Piontkovski *et al.* 2006). On peut alors s'attendre à ce que l'indice NAO influence la durée et l'efficacité des migrations, en termes d'accumulation des réserves. Au cours de notre suivi, l'indice NAO a montré des variations prononcées, avec une phase positive jusqu'à l'hiver 2009-2010 suivie d'une phase négative (**Fig. 3.10**). Bien que nos résultats préliminaires ne montrent pas de relation statistique entre l'indice NAO au cours des différentes migrations et la masse corporelle des femelles (**Fig. 3.9**), la phase négative du NAO coïncide avec la période durant laquelle les femelles ont perdu du poids et où une plus forte proportion de femelles a réalisé une migration de 2 ans (**Fig. 3.10**).

Bien que contre-intuitif, ces résultats sont en accord avec plusieurs études menées chez les serpents, qui montrent que suite à de « mauvaises années », en termes d'abondance de ressources trophiques, il serait préférable de s'engager rapidement dans la reproduction, alors que de « bonnes années » favoriseraient la capitalisation des réserves corporelles et inciteraient à différer la reproduction (Madsen & Shine 1999, Shine 2005).

L'ensemble de ces résultats suggère que chez les tortues luth de Guyane, qui opèrent comme un reproducteur sur capital, il existe un compromis entre la reproduction en cours et les reproductions futures. Nous proposons que ce compromis serait induit par les conditions environnementales rencontrées au cours de la migration, dont dépend la capitalisation des réserves destinées à la reproduction, et qu'il résulterait en une stratégie d'ajustement des durées de migration. Cette stratégie, chez un organisme longévif tel que les tortues luth, pourrait maximiser le succès reproducteur des femelles à long terme.

4. DISCUSSION GENERALE & PERSPECTIVES



L'objectif de ce travail de thèse était de préciser les stratégies de reproduction des tortues marines, en particulier celles des tortues luth nidifiant en Guyane, en répondant aux questions suivantes:

- Comment les tortues marines stockent-elles et gèrent-elles leurs réserves corporelles destinées à la reproduction?
- Comment les caractéristiques maternelles affectent-elles les performances reproductrices ?
- Quels sont les liens entre la migration et la reproduction chez les tortues marines ?

1. Stratégie de stockage des ressources destinées à la reproduction

1.1. Stratégie de stockage et gestion des ressources chez les tortues marines

Le stockage des ressources corporelles destinées à la reproduction est un élément majeur des variations des traits d'histoire de vie (Stearns 1992, Houston *et al.* 2007, Stephens *et al.* 2009). Pourtant, bien que fondamentale dans la compréhension de la diversité des traits liés à la reproduction, la stratégie de stockage des ressources employée par les organismes modèles (reproduction sur capital/ reproduction sur approvisionnement) est souvent supposée *a priori* dans de nombreuses études (Stephens *et al.* 2009). C'est notamment le cas des tortues marines.

En effet, les tortues marines sont communément considérées être des reproducteurs sur capital (Owens 1980, Miller 1997). On pourrait donc se demander **pourquoi chercher à déterminer la stratégie de stockage des ressources destinées à la reproduction chez les tortues marines ?** En réalité pendant une trentaine d'années, le dogme stipulant que les tortues marines sont des reproducteurs sur capital s'est reposé sur le simple fait que les sites d'alimentation sont très distants des sites de reproduction, et que les sites de reproduction, situés en majeure partie aux latitudes tropicales, sont en général des zones peu productives (*i.e.* où les ressources trophiques sont peu abondantes). Ainsi, il était admis que les besoins énergétiques associés à leur reproduction étaient entièrement assurés par les ressources acquises sur les sites d'alimentation. Récemment, ce dogme a pourtant été remis en question par plusieurs études, basées sur des approches biométrique ou comportementale, suggérant que chez plusieurs espèces de tortues marines, les femelles s'alimenteraient au cours de leur saison de ponte (Hoscheid *et al.* 1999, Hays *et al.* 2002, Myers & Hays 2006, Schofield *et al.*

2007, Fossette *et al.* 2008a, Casey *et al.* 2010, Santos *et al.* 2010). Parmi ces études, une majorité a suggéré l'existence d'une stratégie intermédiaire chez la tortue luth (*e.g.* Eckert *et al.* 1989, Myers & Hays 2006, Casey *et al.* 2010), et particulièrement chez la population de tortue luth nidifiant en Guyane (Fossette *et al.* 2007, Fossette *et al.* 2008a, Fossette *et al.* 2009). En effet, en Guyane, la présence de méduses, principales proies des tortues luth, a été rapportée dans les eaux aux abords du site de ponte de la plage de Yalimapo (Fossette *et al.* 2009). De plus, le comportement de plongée des femelles nidifiant sur ce même site de ponte a été décrit comme très actif entre deux pontes, pouvant correspondre à une prospection alimentaire (Fossette *et al.* 2007). Enfin, le déploiement simultané d'enregistreurs de plongée et de capteurs d'ouverture de bec (voir **Boîte 1.3**) a suggéré qu'entre deux pontes ces femelles tenteraient de s'alimenter (Fossette *et al.* 2008a). **Les tortues luth nidifiant en Guyane sont donc un exemple typique de la remise en question du dogme selon lequel les tortues marines sont des reproducteurs sur capital.**

Dans ce travail de thèse, nous nous sommes basés sur une combinaison de deux approches classiques, en réalisant le suivi longitudinal des paramètres biométriques et physiologiques de 35 femelles tortues luth tout au long de leur saison de ponte (**Article 2**). Bien que communément employées, ces approches n'avaient, à notre connaissance, pas encore été conjointement appliquées au cas des tortues marines. La cinétique des paramètres biométriques et physiologiques des femelles tortues luth que nous avons suivies indique qu'elles jeûnent pendant toute leur saison de ponte. Nous ne discuterons pas ici de la mobilisation séquentielle des différents substrats énergétiques, car ce mécanisme est similaire à celui déjà décrit de nombreuses fois chez les mammifères, les oiseaux et les reptiles (*e.g.* Castellini & Rea 1992, Robin *et al.* 1998, Mc Cue 2007). Toutefois, il est intéressant de remarquer que cette adaptation physiologique à la privation de nourriture est commune à une grande diversité d'espèces. **L'ensemble de nos résultats a montré que les tortues luth de Guyane ne s'alimentent pas au cours de leur saison de ponte, et soutient l'hypothèse selon laquelle elles opèrent comme des reproducteurs sur capital.**

Ainsi, malgré la disponibilité en ressources alimentaires (méduses, Fossette *et al.* 2009) aux abords de leur site de ponte, les tortues luth de Guyane n'adopteraient pas une stratégie intermédiaire. Pourtant, compte tenu qu'une tortue luth réalise en moyenne 8 pontes pendant sa longue saison de ponte (*i.e.* 2-3 mois), il paraissait possible qu'un apport alimentaire supplémentaire pendant la reproduction leur permette de compenser leur important effort

reproducteur. Dans les eaux guyanaises, les méduses sont petites (20 gr en moyenne, Fossette *et al.* 2009) et relativement peu abondantes (52 méduses/5min dans 7/36 traits de chalut, Fossette *et al.* 2009) en comparaison des sites d'alimentation (*e.g.* côtes européennes : entre 560g et 2,8 kg en moyenne selon l'espèce, pour une abondance >800 méduses/5min de survol aérien, Houghton *et al.* 2006, Doyle *et al.* 2007). Sachant qu'une méduse est composée à 96% d'eau (Doyle *et al.* 2007), on peut penser qu'**une prospection alimentaire active au cours de la saison de ponte s'avèrerait être une dépense énergétique bien supérieure au gain énergétique apporté par les proies capturées, et donc serait une stratégie inefficace d'un point de vue énergétique.**

Chez la tortue verte, par exemple, il a été suggéré que le recours à un apport alimentaire au cours de la saison de ponte par les femelles serait dépendant des conditions environnementales, *i.e.* de la disponibilité des ressources alimentaires aux abords du site de ponte (Hays *et al.* 2002). Hays *et al.* (2002) montrent que les tortues vertes nidifiant à Chypre s'alimentent pendant la saison de ponte sur les alguiers peu profonds à proximité des plages de ponte, alors que les tortues vertes se reproduisant sur l'île d'Ascension (où il n'y a ni herbier, ni d'alguier) restent au repos au fond de l'eau et assurent leur reproduction grâce à leurs réserves corporelles stockées avant la saison de ponte. Pourtant, si l'on prend pour exemple la population de tortue verte de Mayotte, les femelles qui s'alimentent sur l'herbier au sud de l'île (Ballorain *et al.* 2010) ne se reproduisent pas sur les plages à proximité, pourtant favorables pour la ponte des tortues marines (K Ballorain, communication personnelle). Nous suggérons qu'une approche plus classique, examinant les paramètres physiologiques des femelles, pourrait contribuer à notre compréhension des stratégies de stockage et de gestion des ressources pendant la reproduction des tortues marines.

Par ailleurs, nous proposons une explication alternative aux ouvertures de bec enregistrés au cours des plongées des tortues luth dans l'étude de Fossette *et al.* (2008a) : lors de leur voyage en mer entre deux pontes, les femelles ingéreraient de l'eau afin d'assurer leur hydratation et la maturation des œufs de la ponte suivante.

D'après le suivi physiologique que nous avons réalisé, une question subsiste toutefois quant à l'existence d'un potentiel apport énergétique en supplément des réserves maternelles : en effet, certaines femelles présentaient à leur première ponte des taux élevés de glucose, pouvant suggérer qu'elles étaient dans un état post-absorptif. On peut donc penser que ces

individus se seraient alimentés à la fin de leur migration en direction du site de ponte, ou entre leur arrivée sur le site de reproduction et leur première ponte. A ce stade, la production et la maturation des follicules étant achevée (Rostal *et al.* 1998), nous suggérons que **s’il existe, cet apport alimentaire serait alloué à la maintenance des femelles plutôt qu’à la production de follicules supplémentaires**, comme c’est par exemple le cas chez la couleuvre jarretière (*Thamnophis sirtalis*, Gregory 2006).

Enfin, le comportement en mer des tortues luth de Guyane au cours de la saison de ponte montrant une dispersion importante et des plongées nombreuses (Fossette *et al.* 2007, Georges *et al.* 2007) reste encore à élucider. En effet, il serait plus avantageux pour les femelles, d’un point de vue énergétique, de peu se disperser et de réaliser des plongées de repos, comme cela a été observé par exemple chez les tortues luth du Costa Rica (Reina *et al.* 2005), ou chez les tortues olivâtres de Guyane (**Annexe 3**). Nous proposons que **le comportement de plongée des tortues luth de Guyane pendant leur saison de ponte pourrait être attribué à un comportement d’évitement des prédateurs**. La présence de requins, seuls prédateurs naturels des tortues marines, est connue sur le plateau Guyanais, notamment celle du requin bouledogue (*Carcharhinus leucas*, Formanoir, rapport interne ORSTOM) qui fréquente les embouchures des fleuves, où se trouvent également les tortues luth entre deux pontes (Fossette *et al.* 2007). Cette hypothèse corrobore avec les observations anecdotiques de femelles portant des marques récentes de morsures de requin (VP & JYG, données non publiées).

1.2. Définition de la période de reproduction

La définition de la période de reproduction et comment les ressources sont allouées durant cette période est souvent biaisée par le taxon ou le genre considéré. Il en résulte une complexité à définir et mesurer le degré auquel un organisme est reproducteur sur capital (Stephens *et al.* 2009). Par exemple, chez les animaux qui présentent des soins parentaux post-nataux, les études considèrent généralement différentes portions de la période de reproduction. Ainsi, chez les mammifères, comme les pinnipèdes, les études se concentrent sur la période entre la naissance et le sevrage du jeune (*e.g.* Boyd 2000). Chez les oiseaux, les études considèrent la période de la production de l’œuf (*e.g.* Ward & Bryant 2006) ou la période de la production et de l’incubation de l’œuf (*e.g.* Meijer & Drent 1999). D’autre part,

chez les animaux qui ne présentent pas de soins parentaux post-nataux, comme chez de nombreux squamates, c'est la période qui précède la ponte ou la naissance qui est considérée (e.g. Doughty & Shine 1997). Le choix de la période à laquelle étudier les stratégies de stockage des ressources destinées à la reproduction chez ces organismes en est alors simplifié. Pour pouvoir comparer les différentes stratégies de stockage et de gestion des ressources, une homogénéisation des périodes considérées doit être respectée (Stephens *et al.* 2009). Par exemple, dans le cas des espèces de serpents reproducteurs sur capital, comme la vipère aspic, *Vipera aspis*, de nombreuses études se basant sur la même population ont respecté la même découpe temporelle. Le début de la période de reproduction considérée est la vitellogénèse (e.g. Naulleau & Bonnet 1996, Bonnet *et al.* 2001, Lourdais *et al.* 2002, Lourdais *et al.* 2003). Chez cette espèce, la vitellogénèse commence au sortir de l'hibernation hivernale, dure environ 3 mois, après quoi l'ovulation, la fertilisation et la gestation de la portée se déroulent (Fig. 4.1). Il est alors considéré que si les femelles se nourrissent avant l'ovulation et que cet apport alimentaire participe à l'effort reproducteur en cours, alors ces reproducteurs sur capital s'appuient, dans une certaine mesure, sur un approvisionnement en plus des réserves stockées avant l'hibernation (Bonnet *et al.* 2001, Lourdais *et al.* 2003, Fig. 4.1).

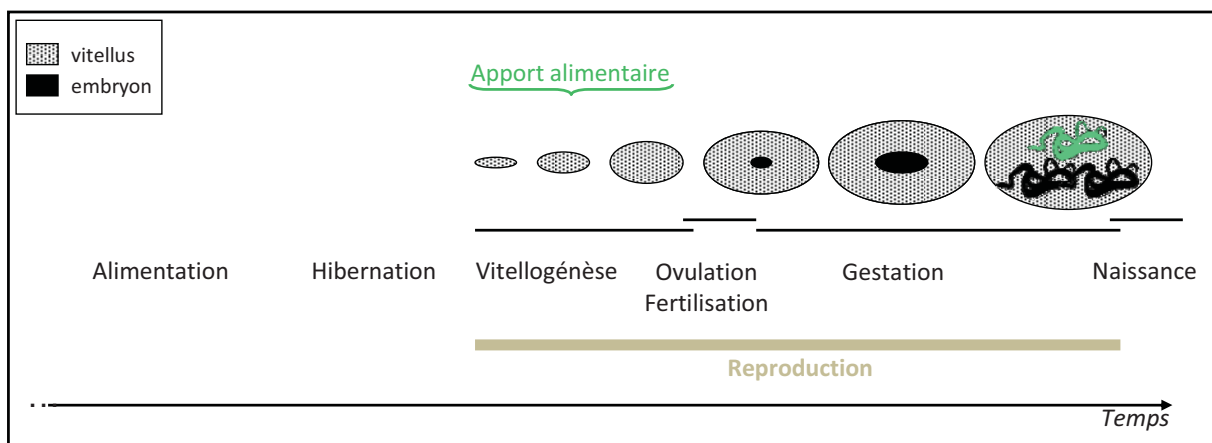


Figure 4.1. Schématisation du cycle reproducteur de la vipère aspic (modifiée d'après Bonnet *et al.* 2001). La période de reproduction (en beige) commence à la vitellogénèse et s'achève à la naissance des vipéreaux. Si la femelle se nourrit pendant la vitellogénèse et que cet apport alimentaire participe à la production de la progéniture (en vert) alors il est considéré que sa reproduction s'est appuyée, dans une certaine mesure, sur un approvisionnement.

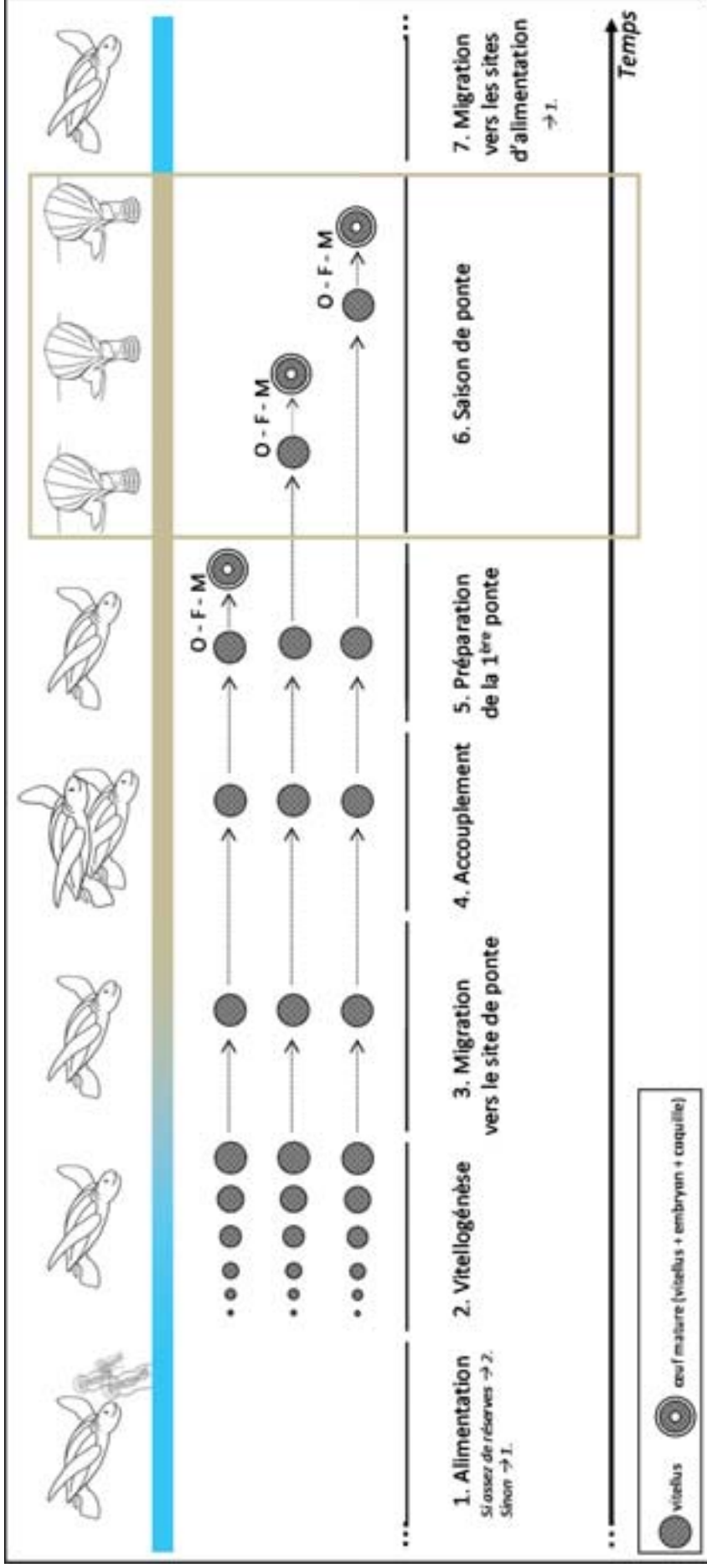


Figure 4.2. Scénario du cycle reproducteur de la tortue luth. La période d'alimentation et de migration en direction du site de ponte figure en bleu. Les processus physiologiques associés à la reproduction débutent avec la vitellogénèse, quand la femelle a stocké suffisamment de réserves corporelles. Lorsque la vitellogénèse est achevée, la femelle migre en direction du site de ponte. Après s'être accouplée, les follicules de la 1^{ère} ponte sont ovulés, puis fertilisés. Quand les œufs sont matures, la femelle vient à terre et entame sa saison de ponte. Après chaque ponte, a lieu l'ovulation des follicules de la ponte suivante, qui seront à leur tour fertilisés et amenés à maturation. La période de reproduction que nous avons définie (encadré beige) dans le cadre de cette thèse s'étend du début à la fin de la saison de ponte. Par soucis de simplification et de clarté, nous avons représenté trois pontes, avec le développement d'un seul œuf par ponte.

O-F-M : Ovulation-Fertilisation-Maturation.

Lorsque l'on considère les tortues marines, une telle distinction est difficilement réalisable. En effet, il est admis que la vitellogénèse se déroule sur les sites d'alimentation (Owens 1980, Miller 1997, Rostal *et al.* 1996, Rostal *et al.* 1998, Hamann *et al.* 2002). Or, le suivi longitudinal des femelles sur leur site d'alimentation puis sur leur site de reproduction est très difficile à réaliser. Par conséquent, la distinction de la nature des ressources allouées à la production des follicules pendant la vitellogénèse, entre les réserves maternelles précédemment stockées et celles acquises au cours de la vitellogénèse est délicate. Toutefois, grâce à une accumulation d'observations de terrain (Owens 1980) et de suivis physiologiques (femelles en semi-captivité, Rostal *et al.* 1996 ; femelles sur site d'alimentation et/ou sur site de reproduction, Rostal *et al.* 1998, Hamann *et al.* 2002), le déroulement de la reproduction des tortues marines et des processus physiologiques associés a pu être décrit. En nous basant sur l'ensemble de ces études, nous pouvons construire le scénario suivant (voir **Fig. 4.2**) : sur le site d'alimentation, les femelles accumulent les réserves dédiées à leur prochaine reproduction. Quand elles ont suffisamment de réserves, la vitellogénèse est initiée, et une rapide recrudescence des follicules a lieu. Le nombre de follicules formés dépend des ressources corporelles que chaque femelle a pu accumuler au préalable. A ce stade, la femelle porte l'ensemble des follicules disponibles pour la saison de ponte à venir, avec autant de classes de follicules qu'il y aura de pontes. Lorsqu'un ensemble de facteurs exogènes (photopériode) et endogènes (niveaux des réserves lipidiques et niveaux hormonaux) est réuni, les femelles peuvent s'engager dans la reproduction et partir en direction des sites de ponte. Une fois arrivées sur le site de reproduction, les femelles présentent une période de réceptivité pendant laquelle les mâles vont pouvoir s'accoupler. La première ovulation a lieu une à deux semaines après les accouplements, puis chaque ponte (jusqu'à l'avant dernière) sera suivie par une ovulation. La fertilisation des ovules et la maturation des œufs de chaque ponte se déroulent après chaque ovulation.

La période de reproduction doit être déterminée dans chaque cas en particulier (Stephens *et al.* 2009). Selon la définition de reproducteur sur capital, le capital représente une accumulation de nutriments déposés sous forme de réserves corporelles maternelles avant la ponte (Thomas 1988). Chez les tortues marines, bien que la vitellogénèse se déroule sur le site d'alimentation, il est admis qu'elle repose sur les réserves acquises au préalable, et qu'elle est achevée avant le départ pour le site de reproduction (Owens 1980, Rostal *et al.* 1996, Miller 1997, Rostal *et al.* 1998). Compte tenu de leur cycle de vie et de la physiologie de leur reproduction (**Fig. 4.2**), nous considérons donc que **la période de reproduction que nous**

avons définie, *i.e.* du début à la fin de la saison de ponte, est pertinente dans le cadre de l'étude de la stratégie de stockage et gestion des ressources des tortues marines.

1.3. Déterminants des stratégies de stockage et de gestion des ressources

Plusieurs paramètres déterminant les stratégies de stockage et de gestion des ressources ont été décrits dans la littérature afin de placer un organisme sur le continuum reproduction sur capital/reproduction sur approvisionnement (**Fig. 4.3**). Dans un premier temps, les organismes semélipares peuvent être considérés comme l'exemple extrême qu'une reproduction sur capital. Un deuxième critère de distinction se base sur le métabolisme des organismes : de manière générale il est considéré que les endothermes sont plutôt des reproducteurs sur approvisionnement, et les ectothermes des reproducteurs sur capital (Bonnet *et al.* 1998). En effet, comme nous l'avons vu dans l'introduction, ces organismes présentent des prédispositions pour l'adoption de la stratégie sur capital (Bonnet *et al.* 1998). Cependant, tous les ectothermes ne sont pas des reproducteurs sur capital (par exemple, les lézards de petite taille). De plus, les études s'intéressant aux oiseaux et aux mammifères ont souvent rapporté que la taille corporelle adulte (relative à la famille considérée) est un facteur déterminant de la stratégie de stockage et de gestion des ressources adoptée (*e.g.* Drent & Daan 1980, Boyd 1998, Klaassen 2001). Toutefois, basés sur ces critères, certains organismes dits reproducteur sur capital se sont révélés adopter une stratégie intermédiaire (*e.g.* Wheatley *et al.* 2008, Sénéchal *et al.* 2011). Houston *et al.* (2007) ont alors proposé un modèle théorique (basé sur les mammifères) permettant de positionner un organisme sur le continuum reproducteur sur capital/reproducteur sur approvisionnement. Selon ces auteurs, la masse corporelle (ou la taille) seule ne peut expliquer le choix d'une stratégie ou de l'autre. Ils soulignent l'importance des coûts associés à l'accumulation d'un capital (*i.e.* coûts de stockage), à la durée et aux contraintes associées à la période de gestation et de lactation et à la masse et au métabolisme de la progéniture. Ainsi, Houston *et al.* (2007) concluent que ces coûts sont le déterminant majeur dans le choix d'une stratégie, et peuvent mener à une stricte reproduction sur approvisionnement, une stricte reproduction sur capital ou une combinaison des deux.

Bien que très commode, le modèle théorique proposé par Houston *et al.* (2007) ne peut pas s'appliquer à l'ensemble des organismes, et notamment dans le cas des espèces itéropares, qui au cours d'un épisode reproducteur produisent plusieurs pontes. C'est le cas des tortues marines, et de certaines espèces de lézards. A notre connaissance, peu d'études se sont

intéressées à ces modèles. Dans le cas des lézards produisant plusieurs pontes au cours d'un épisode reproducteur, il semblerait que plusieurs stratégies soient employées. Chez le lézard *Amphibolurus muricatus*, par exemple, la production des œufs repose sur les réserves maternelles pour les lipides, et sur un apport alimentaire supplémentaire pour les protéines (Warner *et al.* 2007). Par contre, chez les lézards à collier, l'ensemble de la production des œufs repose sur les réserves endogènes de la femelle, et un apport alimentaire supplémentaire serait alloué vers la croissance maternelle (Telemeco & Baird 2011). Concernant les tortues marines, compte tenu des études réalisées à ce jour, nous ne pouvons statuer que sur le cas des tortues luth. Ainsi, en considérant les déterminants cités ci-dessus et nos résultats, **nous plaçons la tortue luth de Guyane sur le continuum des stratégies de stockage vers l'extrémité décrite pour la reproduction sur capital (Fig. 4.3).**

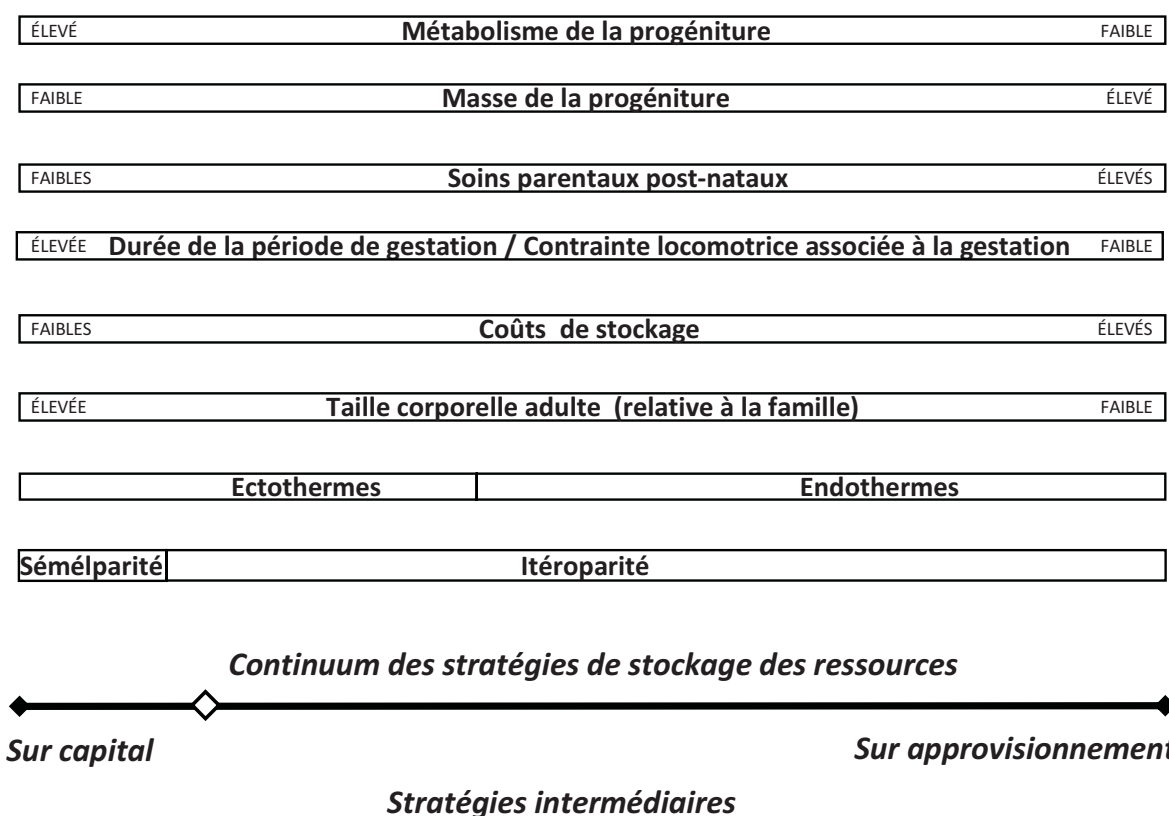


Figure 4.3. Schématisation des déterminants des stratégies de stockage des ressources d'après la littérature. Basés sur les critères applicables aux tortues marines et sur nos résultats, la place de la tortue luth de Guyane (losange blanc) se situe vers l'extrême « reproduction sur capital » sur le continuum reproduction sur capital/reproduction sur approvisionnement.

2. Traits maternels et effort reproducteur

2.1. Taille et condition corporelle

Comme nous l'avons vu dans l'introduction, les traits parentaux, et en particulier maternels, influencent l'effort reproducteur de la reproduction en cours. Que les organismes soient reproducteurs sur capital ou sur approvisionnement, la taille et la condition corporelle sont généralement considérées comme les traits maternels qui exercent une forte contrainte sur la reproduction, aussi bien chez les mammifères (*e.g.* Festa-Bianchet *et al.* 1998, Georges & Guinet 2000), les oiseaux (*e.g.* Chastel *et al.* 1995a, Vleck & Vleck 2002), les poissons (*e.g.* Hussey *et al.* 2010, Donelson *et al.* 2008) que chez les reptiles (*e.g.* Lourdais *et al.* 2002, Litzug *et al.* 2008). De plus, chez les reproducteurs sur capital, outre la possible contrainte physique imposée par la taille à un instant donné (Vitt & Congdon 1978), la condition corporelle maternelle en début de reproduction détermine en majeure partie la production de la progéniture (Bonnet *et al.* 2001). Ainsi, chez certains reproducteurs sur capital, l'existence d'un seuil minimum de condition corporelle (au stade pré-vitellogénique) que la femelle doit dépasser afin de pouvoir s'engager dans la reproduction a été décrite (*e.g.* la vipère aspic, Naulleau & Bonnet, 1996). Chez les reproducteurs sur approvisionnement, la relation entre la condition corporelle maternelle en début de reproduction et l'effort reproducteur est moins forte (Bonnet *et al.* 2001).

Chez les reproducteurs sur capital, chez qui, par définition, une importante partie des réserves corporelles maternelles est allouée dans la production de la progéniture, le ratio [masse totale de la progéniture/masse maternelle] est généralement élevé. Par exemple, chez la vipère aspic, la masse de la portée représente environ 34% de celle de la femelle en début de reproduction (calcul d'après Lourdais *et al.* 2002). Chez l'iguane marin des Galápagos (*Amblyrhynchus cristatus*), la masse totale des œufs pondus lors de l'unique ponte de l'épisode reproducteur représente de 25 à 30% de la masse maternelle (Wikelski & Romero 2003). Enfin, chez les tortues marines, la masse totale des œufs pondus au cours d'une saison de ponte représente entre 10 et 20% de la masse initiale maternelle (Wallace *et al.* 2007), en accord avec nos résultats chez la tortue luth (15%). Ainsi, la reproduction sur capital est particulièrement coûteuse pour les femelles. A titre indicatif, chez les reproducteurs sur approvisionnement, cette proportion est plus modérée et variable: par exemple, chez les manchots royaux, la masse de l'œuf représente 3% de la masse de la femelle en début de reproduction (Barrat 1976), et chez l'otarie d'Amsterdam (*Arctocephalus tropicalis*), la masse du jeune correspond

à 10% de la masse maternelle (Georges & Guinet 2000). Toutefois, la comparaison s'avère être difficile car compte tenu que le métabolisme basal est plus important chez les endothermes (mammifères, oiseaux) que chez les ectothermes (reptiles) (Nagy *et al.* 1999), on peut *a priori* supposer que les coûts énergétiques associés à la production d'un jeune mammifère est plus élevé que la production d'un œuf ou d'un jeune reptile.

2.2. Chez les tortues marines

Traits maternels biométriques

Chez les tortues marines, les études s'intéressant à la relation entre les traits maternels et la performance de reproduction ont principalement examiné la relation entre la taille maternelle (*i.e.* la longueur de carapace) et la masse ou le nombre de la progéniture (*e.g.* Bjorndal & Carr 1989, Hays & Speakman 1991, Van Buskirk & Crowder 1994, Price *et al.* 2004). Ces études présentent des résultats contradictoires : alors que Van Buskirk & Crowder (1994) montrent chez chacune des sept espèces de tortues marines l'existence d'une relation positive entre la taille maternelle et le nombre d'œufs pondus au cours d'une saison, Reina *et al.* (2002) et Wallace *et al.* (2007) ne trouvent pas de telle relation chez les tortues luth du Costa Rica. Toutefois, une autre étude portant sur la même population de femelles, mais reposant sur un jeu de données moins important, montre un effet positif de la longueur maternelle sur la taille des pontes (Price *et al.* 2004), laissant supposer que cette relation peut être compromise par un biais d'échantillonnage. Wallace *et al.* (2007) proposent que d'autres caractéristiques maternelles, comme la masse corporelle, doivent avoir un effet plus important sur la performance reproductrice de la tortue luth. Pourtant à notre connaissance, aucune étude n'a examiné la relation entre la masse corporelle maternelle et la performance de reproduction chez les tortues marines. Peser une tortue marine adulte, et particulièrement les tortues luth, présente des difficultés logistiques (temps, personnel). Dans le présent travail, la masse corporelle maternelle en début de saison de ponte explique 27% de la masse totale des œufs pondus dans la saison (**Article 2**). Ces résultats supportent l'hypothèse de Wallace *et al.* (2007).

Par ailleurs, nous avons montré que la condition maternelle en début de saison explique 41% de la masse totale des œufs pondus dans la saison. De plus, nous avons identifié un seuil de condition corporelle en début de saison en deçà duquel les femelles altèrent considérablement leur condition pendant la saison de ponte (**Article 2**). Nous suggérons alors que les femelles tortues luth devraient également dépasser un seuil de condition corporelle avant l'initiation de la vitellogénèse pour pouvoir s'engager dans la reproduction. Cette hypothèse corrobore les

autres études sur la physiologie de la reproduction des tortues marines (**Fig. 4.2**, Owens 1980, Rostal *et al.* 1996, Miller 1997, Rostal *et al.* 1998).

Traits maternels moléculaires

Pour pallier aux potentielles difficultés logistiques associées à la mesure de la masse des tortues marines adultes, nous nous sommes intéressés à un nouvel indice moléculaire : la taille des télomères. Nous avons ainsi montré (**Article 4**) qu'à l'échelle d'une saison de reproduction, la taille des télomères est un meilleur indice de la performance de reproduction que la condition maternelle. A l'instar d'autres études récentes démontrant chez les oiseaux que les télomères constituent un bon prédicteur de la survie (Bize *et al.* 2009) ou du succès reproducteur à l'échelle de la vie (Pauliny *et al.* 2006), notre étude contribue à l'idée selon laquelle les télomères sont un outil moléculaire prometteur dans le domaine de l'écologie (Monaghan 2010). Cependant, son utilisation sur les tortues marines reste novatrice, et nécessite de plus amples études.

Toutefois, ni la longueur des télomères, ni la condition corporelle maternelle ne semble expliquer en totalité la performance de reproduction. Une autre hypothèse, non exclusive, est que la variation inter-individuelle des performances de reproduction pourrait être dépendante des différentes conditions environnementales expérimentées par les femelles.

3. Les migrations des tortues marines

Au cours de ce travail de thèse, nous avons pu avoir accès indirectement à ce qui se passe en mer pendant les migrations des tortues luth nidifiant en Guyane. Nous avons ainsi pu déterminer les capacités de stockage des femelles et définir les liens entre leur migration et leur reproduction.

3.1. Stockage des ressources

Les capacités d'un individu à extraire les ressources de son environnement affectent la quantité d'énergie qu'il pourra allouer aux différentes fonctions de vie (Boggs 1992). Chez les tortues marines, c'est lors de leurs migrations pluri-annuelles que les femelles restaurent et stockent les réserves corporelles nécessaires à la reproduction (Miller 1997). Au cours de ces

migrations, les femelles tortues luth nidifiant en Guyane se dispersent dans tout l'Atlantique Nord (Ferraroli *et al.* 2004, Fossette *et al.* 2010a, **Annexe 1**) et exploitent les domaines néritiques et océaniques (Fossette *et al.* 2008c, Fossette *et al.* 2010a, **Annexe 1**). L'accès direct aux femelles pendant ces migrations est donc très difficile. Dans le cadre de cette thèse, nous avons pu avoir accès aux paramètres biométriques de femelles tortues luth sur un de leur site d'alimentation connu au large des côtes Est Canadiennes (James *et al.* 2005). Nous avons ainsi pu estimer (**Article 1 ; Partie 3, Section 1**) qu'en une centaine de jours de résidence sur ce site d'alimentation, les tortues luth sont capables de prendre une centaine de kilogrammes. Cette estimation indique donc qu'une femelle moyenne de 400 kg (Georges & Fossette 2006) pourrait grossir du quart de son poids. De 2007 à 2010, Heaslip *et al.* (2012) ont équipé de caméra 17 tortues luth sur leur site d'alimentation au large de la Nouvelle Ecosse (côtes Est Canadiennes) dans le but d'examiner leur comportement alimentaire. Les auteurs ont ainsi pu montrer que les tortues luth ingèrent en moyenne 330 kg de méduses (*Cyanea capillata*) par jour, soit 13 kg de matière organique (Doyle *et al.* 2007). Le taux d'efficacité de transfert entre deux niveaux trophiques étant de 10% (Lindeman 1942), ceci équivaldrait finalement à une prise de poids quotidienne d'environ 1kg, comme nous l'avons estimé.

Nous avons montré qu'une migration de 2 ans est suffisante pour que les femelles restaurent leurs réserves pour le prochain épisode reproducteur (**Partie 3, Section 3.2**). On peut alors se demander pourquoi certaines femelles réalisent des migrations de 3 ans. Une hypothèse serait que l'accumulation de réserves au cours d'une année supplémentaire en migration demande aux individus une plus grande capacité volumique. En effet, cette contrainte physique a été observée chez les tortues aquatiques (*e.g.* Tucker *et al.* 1998), de même que chez les lézards (*e.g.* Du *et al.* 2005) et les serpents (Shine 2003). Toutefois, dans notre étude, les femelles réalisant une migration de 2 ans ne sont pas plus petites que celles réalisant une migration de 3 ans (données non présentées). L'hypothèse de contraintes physiques n'est donc pas validée chez les tortues luth de Guyane.

De plus, au cours de notre suivi longitudinal sur trois saisons de pontes successives (**Partie 3, Section 3.2**), nous avons montré que les femelles qui réalisent une migration de 3 ans reviennent pondre avec 18 kg de plus que les femelles qui réalisent une migration de 2 ans. Ce gain de masse en une année supplémentaire est pourtant bien plus faible que le gain de 1kg/j estimé sur site d'alimentation. Cette différence peut s'expliquer par le simple fait qu'au cours des migrations, les conditions trophiques ne sont pas constantes. En effet, la période de

reproduction des cnidaires en milieux tempérés donne lieu à la production des méduses au printemps ou à l'automne (Chudnow 2008). Par conséquent, la disponibilité des ressources trophiques est saisonnière, ce qui implique qu'au cours de leur migration : i) les tortues luth ne s'alimentent pas en continu à des rythmes aussi importants que ce que nous avons observé sur site d'alimentation, et ii) les tortues luth ne restent pas sur le même site d'alimentation. En effet, les suivis télémétriques ont montré que pendant leurs migrations, les femelles tortues luth ajustent constamment leurs déplacements en fonction des conditions océanographiques locales, ce qui les amène à changer de site d'alimentation (Hays *et al.* 2006, Fossette *et al.* 2010b).

Enfin, nous suggérons que la décision de se reproduire après 2 ou 3 ans de migration serait induite par une contrainte énergétique, comme c'est le cas chez certains reptiles (*e.g.* Naulleau et Bonnet 1996, Olsson & Shine 1997, Rollinson & Brooks 2008). Cette contrainte énergétique peut dépendre de l'efficacité prédatrice des individus et/ou des conditions environnementales (*i.e.* disponibilité des ressources trophiques).

3.2. Migration et reproduction

3.2.1. Le paradoxe des tortues luth

De manière générale, les animaux qui retardent leur saison de reproduction (Bull & Shine 1979, Clutton-Brock 1998) mettent à profit ce temps supplémentaire pour acquérir un surplus d'énergie, qui pourra être alloué à la reproduction, afin d'améliorer la performance de reproduction du prochain épisode reproducteur (Smith & Fretwell 1974, Bonnet *et al.* 2001). Bien que, chez les tortues luth de Guyane, différer la saison de reproduction d'une année, en réalisant une migration plus longue (*i.e.* 3 ans), soit proportionnellement plus profitable pour les femelles, en termes de gain de masse, et moins coûteuse, nous avons montré que les femelles réalisent majoritairement des migrations plus courtes (*i.e.* 2 ans). Cependant, en se reproduisant tous les deux ans les femelles pourraient, au terme de leur vie, réaliser un effort reproducteur plus important, et pourraient donc avoir un succès reproducteur plus élevé à l'échelle de leur vie (**Fig. 4.4**).

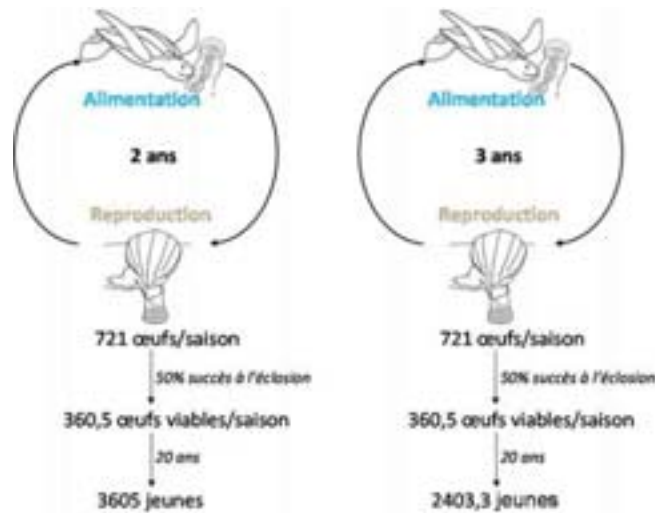


Figure 4.4. Estimation du succès de reproduction des tortues luth de Guyane au bout de 20 années de reproduction, selon le mode de migration adopté (2 ans vs 3 ans). Ces calculs sont basés sur la performance de reproduction moyenne (Article 2) et le taux moyen de succès à l'éclosion rapporté chez les tortues luth (Rafferty *et al.* 2012b).

La « décision » de s'engager dans la reproduction des tortues luth de Guyane semble être réalisée à deux échelles de temps. Premièrement, à l'échelle d'un cycle reproducteur, le facteur proximal est la masse corporelle, *i.e.* la condition (Article 2 ; Partie 3, Section 3.2). Deuxièmement, à l'échelle de la vie, les tortues luth étant des organismes longévifs itéropares, réalisent un compromis entre la reproduction en cours et les futures reproductions. Nous proposons que ce compromis dépend de l'établissement du capital de réserves destinées à la reproduction et qu'il serait induit indirectement par les conditions environnementales rencontrées lors de la migration. En effet, nous suggérons que les femelles ajusteraient la durée de leur migration en fonction des conditions environnementales. Toutefois, alors qu'il semble plus logique de différer la reproduction quand les conditions environnementales sont moins favorables, nous avons montré que lors des « mauvaises années », les tortues luth réalisent de manière préférentielle des migrations plus courtes. On peut penser que cette « décision » permettrait de limiter les risques de passer une année supplémentaire en mer où les ressources trophiques sont défavorables. Cependant, si les conditions en mer sont défavorables sur une longue période de temps, il est probable qu'en réalisant des migrations de 2 ans, les femelles soient contraintes d'ajuster (*i.e.* d'abaisser) leur seuil de condition corporelle et donc de s'engager dans la reproduction avec un capital de réserves insuffisant, tel que cela a été montré chez le python d'eau (*Liasis fuscus*, Madsen & Shine 1999). Dans ce cas, les femelles pourraient par la suite réaliser une migration de 3 ans, si les conditions le permettent, afin de restaurer leur condition corporelle. Cette hypothèse expliquerait pourquoi

certaines femelles alternent, au cours de leur histoire de reproduction, entre des migrations de 2 ans et de 3 ans. Pour tester cette hypothèse chez les tortues luth de Guyane, il serait nécessaire de réaliser un suivi à long terme.

3.2.2. Importance des conditions environnementales

La disponibilité des ressources trophiques, et particulièrement dans les écosystèmes marins, est sous l'influence des oscillations climatiques telles que celles représentées par l'indice ENSO pour l'océan Pacifique (*El Niño Southern Oscillation*) ou l'indice NAO pour l'océan Atlantique (Stenseth *et al.* 2002, Stenseth *et al.* 2003). De nombreuses études ont en effet montré l'influence de ces indices climatiques sur les populations d'oiseaux, de poissons ou de planctons (*e.g.* Russel *et al.* 1971, Aebischer *et al.* 1990, Fromentin & Planque 1996, Lehodey *et al.* 1997, Barton *et al.* 2003, Barrett *et al.* 2012). Les variations climatiques associées à ces indices agissent sur les individus et les populations en opérant à différents niveaux, soit directement *via* les processus physiologiques, ou soit indirectement *via* les réseaux trophiques (Stenseth *et al.* 2002).

La tortue luth est le prédateur terminal d'une chaîne trophique courte (phytoplancton > zooplancton > zooplancton gélatineux > tortue luth). Les effets du climat sur la production primaire et secondaire des réseaux trophiques marins étant intégrés par les plus hauts maillons des chaînes trophiques (*bottom-up forcing*, Croxall *et al.* 1988, Frederiksen *et al.* 2006), la tortue luth sera donc particulièrement sensible aux fluctuations environnementales (Fig. 4.5, Saba *et al.* 2008).

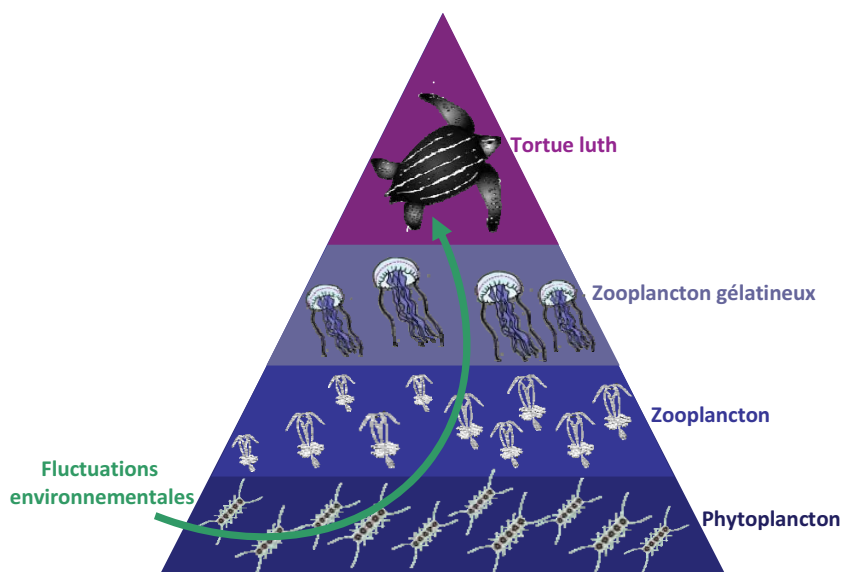


Figure 4.5. Illustration de l'effet « bottom-up » au sein du réseau trophique de la tortue luth : les fluctuations environnementales peuvent modifier le réseau trophique depuis les échelons inférieurs vers les échelons supérieurs.

Plusieurs études ont récemment montré chez les tortues luth nidifiant dans la région du Pacifique Est, que leur durée de migration résulte de la variabilité de la disponibilité des ressources trophiques de l'océan Pacifique sous l'influence de l'indice climatique ENSO (Saba *et al.* 2007, Wallace & Saba 2009, Reina *et al.* 2009) : lors des années El Niño, la disponibilité des ressources est faible, induisant des migrations plus longues. La situation inverse est observée lors des années la Niña. A notre connaissance, seul Rivalan (2004) s'est intéressé à l'influence des conditions climatiques sur l'écologie de la reproduction des populations de tortues marines dans l'Atlantique : il a montré que l'indice NAO influence la durée de la saison de ponte et le nombre de pontes produites par saison des tortues luth de Guyane. Au cours de ce travail, nous avons utilisé l'indice NAO afin d'examiner l'impact des conditions environnementales sur la masse corporelle des tortues luth de Guyane, leur performance de reproduction et par conséquent sur leur stratégie de reproduction. Bien que nous n'ayons pas réussi statistiquement à montrer d'influence directe du NAO sur la reproduction des tortues luth, les variations de la masse corporelle des femelles au cours du temps covarient remarquablement avec l'indice NAO (**Fig. 3.10**).

L'indice NAO présente l'avantage d'être facilement accessible. Cependant, il est possible qu'il ne soit pas le meilleur indice reflétant la disponibilité des ressources trophiques exploitées par les tortues luth à l'échelle de l'océan Atlantique. En effet, l'impact de l'indice NAO sur les écosystèmes marins diffère selon les régions de l'océan Atlantique, selon les espèces considérées, et peut agir avec un décalage temporel (Parsons & Lear 2001, Barton *et al.* 2003, Greene *et al.* 2003, Piontkovski *et al.* 2006). Partant de l'hypothèse communément admise selon laquelle l'abondance en plancton gélatineux (*i.e.* méduses) est proportionnelle à la production primaire nette (NPP, Saba *et al.* 2008), on pourrait utiliser cette mesure de NPP comme indice des conditions trophiques de l'océan Atlantique. De plus, d'après des études télémétriques, les tortues luth nidifiant en Guyane exploitent trois régions distinctes de l'Atlantique Nord pendant leur migration : le Nord Ouest, le Nord Est et l'Est Equatorial (Ferraroli *et al.* 2004, Fossette 2010a, **Annexe 1**). La juxtaposition de la carte illustrant les zones d'alimentation principales des tortues luth (Fossette 2010a, **Annexe 1, Fig. 4.6.a**) avec la carte de productivité primaire nette dans l'océan Atlantique (Saba *et al.* 2008, **Fig. 4.6.b**), montre d'une part, que les tortues luth rencontrent des conditions trophiques contrastées au cours de leur migration et d'autre part, que les zones d'alimentation principales concordent remarquablement avec les zones les plus productives (**Fig. 4.6**). Par conséquent, notre hypothèse semble correcte, et on pourrait s'attendre à ce que la production primaire nette calculée sur ces zones influence la reproduction des tortues luth nidifiant en Guyane.

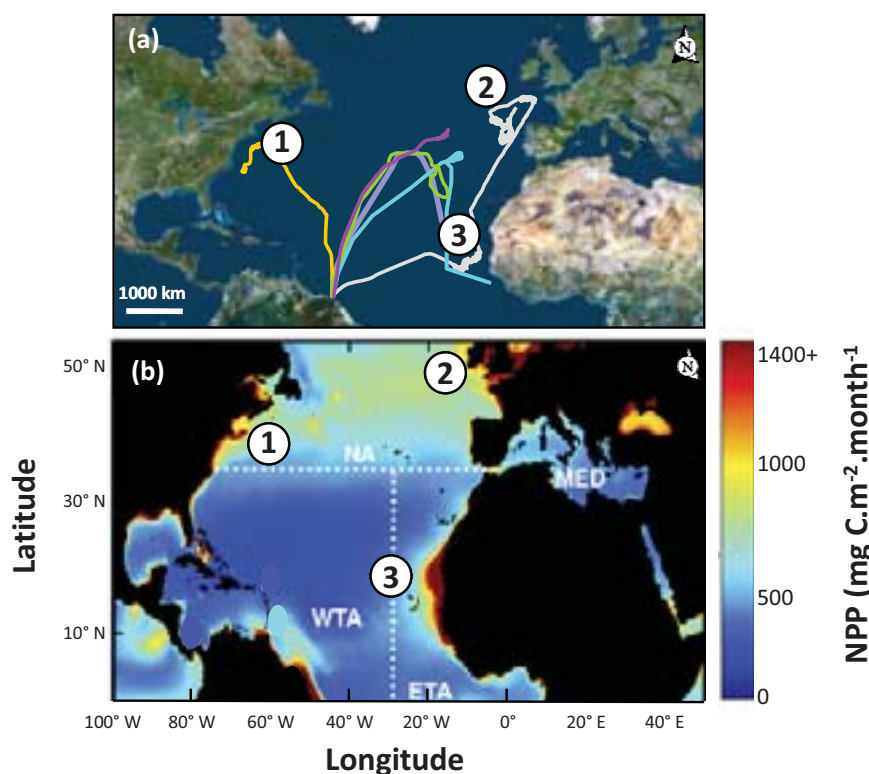


Figure 4.6. Zones exploitées par les tortues luth nidifiant en Guyane définies par suivis télémétrique Argos (a, d'après Fossette *et al.* 2010a, Annexe 1) et productivité primaire nette des différents bassins de l'Atlantique Nord (b, d'après Saba *et al.* 2008). Cette figure illustre le chevauchement des zones d'alimentation avec les zones les plus productives (*i.e.* où la production primaire nette (NPP) est élevée).

Par ailleurs, une étude récente basée sur une analyse isotopique propose que la durée des migrations des tortues luth nidifiant en Guyane est tributaire de la zone géographique qu'elles exploitent : les tortues réalisant des migrations de 3 ans exploiteraient la zone Est Equatoriale (point 3, **Fig. 4.6.a**), alors que les tortues réalisant des migrations de 2 ans exploiteraient des zones plus boréales (points 1 et 2, **Fig. 4.6.a**, Caut *et al.* 2008). En suivant cette hypothèse, on s'attendrait à ce que les zones exploitées lors des migrations plus longues (*i.e.* les zones équatoriales) soient réalisées dans des zones moins productives. Toutefois, cette correspondance ne semble pas évidente au regard de la carte des NPP moyennes sur les trois différents zones d'alimentation principales de l'Atlantique Nord (**Fig. 4.6.b**). Afin de mieux comprendre les liens possibles entre la durée et la localisation des migrations, des études complémentaires pourraient consister à comparer la production primaire nette, calculée séparément pour ces grands domaines océaniques lors des migrations de 2 et 3 ans. Enfin, une autre possibilité, non-exclusive, pourrait être que les femelles qui réalisent une migration de 3 ans exploiteraient dans un premier temps les zones d'alimentation boréales puis, sur le retour

vers le site de ponte, les zones équatoriales, comme le suggère le trajet d'une femelle obtenu par suivi Argos représenté en gris clair sur la **Fig. 4.6.a**.

D'autres études ont également rapporté qu'en influençant la durée des migrations des tortues marines, les conditions environnementales avaient un impact sur les effectifs annuels des femelles reproductrices, et par conséquent sur la dynamique des populations (*e.g.* Broderick *et al.* 2001, Solow *et al.* 2002, Saba *et al.* 2008, Reina *et al.* 2009). Au cours de cette thèse, les saisons de pontes 2008 et 2009 (Saison S2, **Fig. 3.10**) ont été marquées par un nombre particulièrement élevé de femelles venues pondre à Yalimapo, dont plus de 40% étaient des femelles primipares (JYG & V Plot, **Fig.4.7**, données non publiées). Nous proposons que les conditions environnementales favorables qui ont caractérisé la migration précédant ces saisons (**Fig. 3.10**) auraient permis à ces jeunes femelles d'acquérir une condition corporelle particulièrement bonne, ce qui les auraient amenées à s'engager dans leur première reproduction.

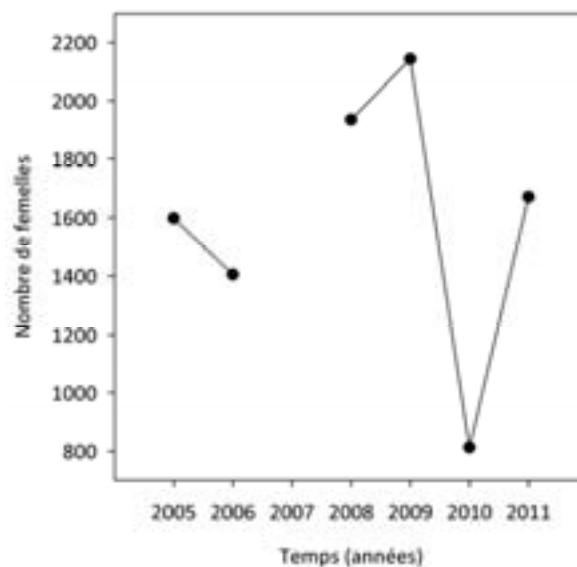


Figure 4.7. Nombre de femelles venues pondre sur la plage de Yalimapo comptabilisées au cours de notre suivi de 2005 à 2011 (à l'exception de 2007) (JYG &VP données non publiées).

L'ensemble des grandes conclusions issues de ce travail de thèse est synthétisé dans la Figure 4.8 ci-dessous.

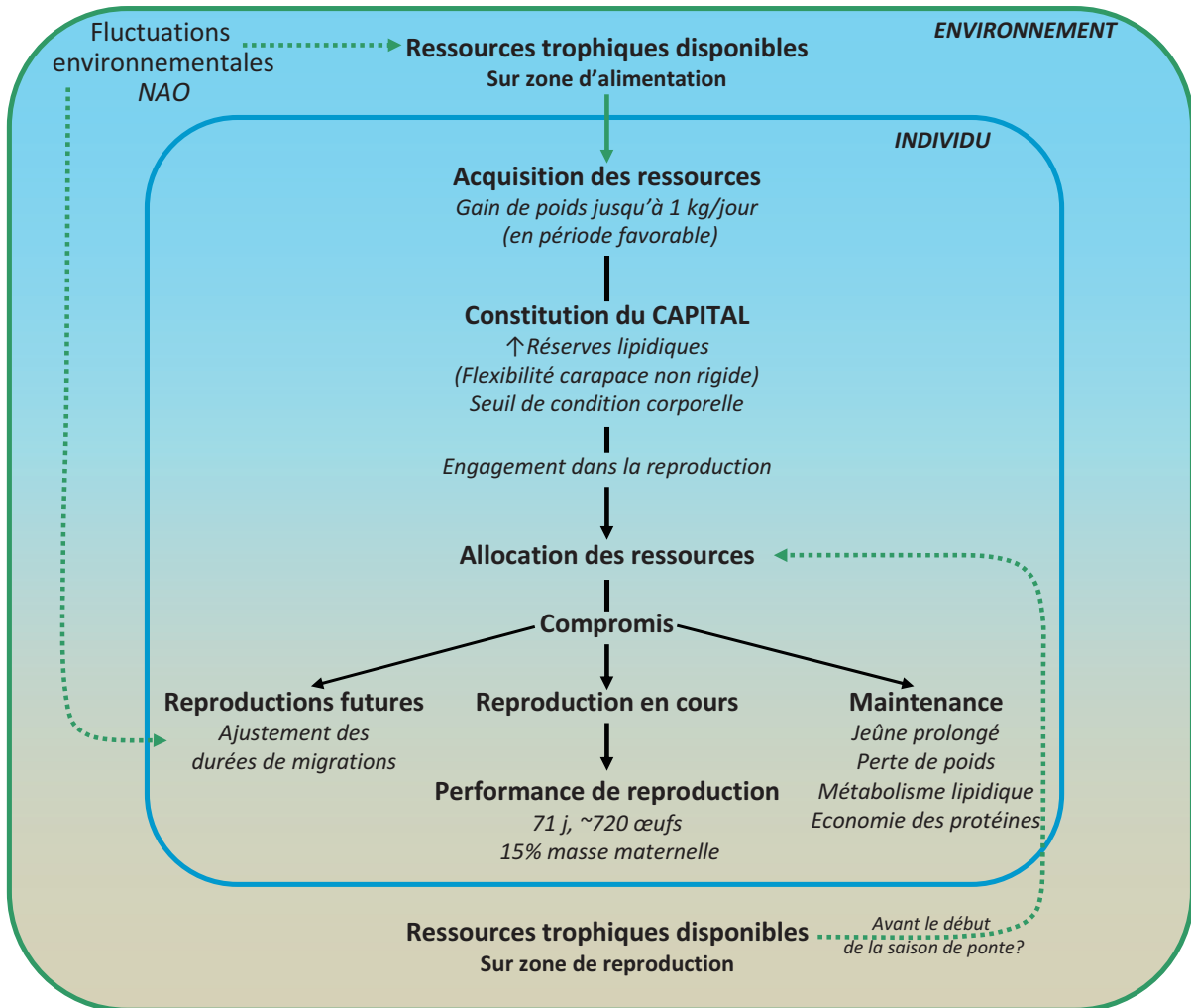
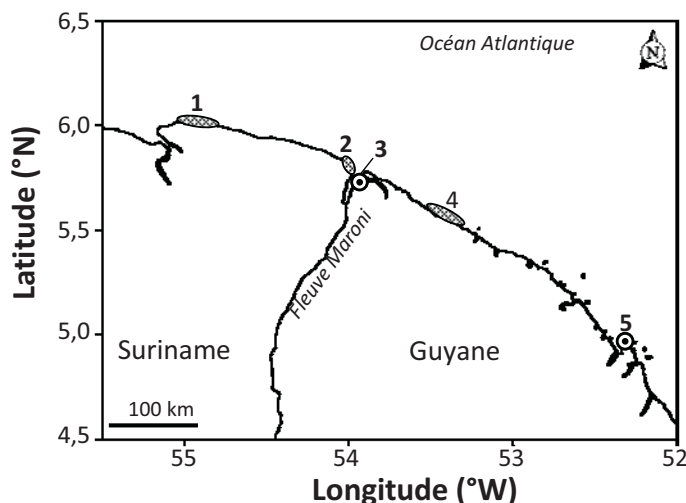


Figure 4.8. Schématisation de la synthèse des grandes conclusions issues de la thèse illustrant les liens établis (—) et possibles (···) entre les conditions environnementales et les stratégies d'acquisition, de stockage et d'allocation des ressources destinées à la reproduction chez les tortues luth de Guyane, à l'échelle d'un cycle de reproduction, comprenant la période de migration (bleu) et la période de reproduction (beige).

4. Regard critique de notre étude

4.1. Zone de suivi de la reproduction

Notre suivi est basé sur un protocole de capture-marquage-recapture, pour lequel au moins deux limites peuvent être envisagées : i) la période de suivi peut être insuffisante pour observer toutes les femelles venant se reproduire sur la plage ; et ii) des femelles peuvent se reproduire en dehors de la plage de Yalimapo. Dans le premier cas, compte tenu que nous sommes présents de début Mars à fin Juillet, soit l'intégralité de la période de ponte des tortues luth, la probabilité que des femelles ne soient pas observées au cours de leur saison de ponte est faible (Rivalan *et al.* 2005). Dans le deuxième cas, notre zone d'étude étant limitée à une portion de plage de 4km, il est possible que des femelles aillent pondre sur d'autres plages. En effet, les comptages de pontes réalisés le long du littoral guyanais révèlent l'existence d'une activité de ponte sur des plages isolées (Fig. 4.9). Cependant, à titre d'exemple, en 2008, les pontes (et non les femelles) répertoriées sur ces plages isolées ne représentaient que 3,5% des pontes enregistrées sur la plage de Yalimapo (calcul réalisé à partir du bilan 2008 des pontes de tortues marines en Guyane, Berzin *et al.* 2009). Nous estimons donc que notre marge d'erreur reste négligeable. D'autre part, sur les 300 femelles que nous avons suivi depuis 2005, seules 7 ont été observées pondre à Cayenne (n=1) ou au Suriname (n=6) (Fig. 4.9) au cours d'une saison pendant laquelle elles ont également été observées sur la plage de Yalimapo. De plus, le suivi réalisé sur les plages de Cayenne révèle une très faible proportion d'individus communs aux deux sites de ponte (1 femelle par saison, B de Thoisy, données non publiées). Ainsi, nous pouvons être confiants quand au caractère exhaustif de notre suivi de la reproduction des tortues luth.



4.2. Stratégies de reproduction et succès reproducteur à l'échelle de la vie

Les compromis entre la reproduction en cours et les reproductions futures peuvent influencer le succès reproducteur au terme de la vie, particulièrement chez les organismes longévifs (Shaffer 1974). Dans ce travail, nous suggérons que les tortues luth effectuent un tel compromis en ajustant la durée de leur migration, de sorte qu'au cours de leur vie, elles ont plus d'opportunités de se reproduire et donc un succès reproducteur plus important au terme de la vie. Toutefois, nous ne connaissons que la performance de reproduction des femelles, alors que pour calculer le succès reproducteur au terme de la vie, nous aurions besoin du taux de succès à l'éclosion, celui-ci étant dépendant des années, et des femelles considérées (Rafferty *et al.* 2012b). Nous ne pouvons donc pas, à proprement parler, estimer quel est l'effet de ce compromis sur le succès reproducteur au terme de la vie.

5. Perspectives

Ce travail apporte une contribution à l'étude des stratégies de reproduction des tortues marines. Nous avons pu en aborder divers aspects, mais de nombreuses questions restent à aborder. Nous proposons ici quelques pistes de futures études complémentaires.

5.1. Les tortues luth, des reproducteurs sur capital au sens strict ?

Suite à ce travail de thèse, il semble évident que les tortues luth nidifiant en Guyane opèrent comme des reproducteurs sur capital. Toutefois, une question subsiste quand à la possibilité d'un apport alimentaire supplémentaire aux abords du site de ponte avant la première ponte. La méthode basée sur l'analyse des isotopes stables pourrait nous apporter ce dernier élément de réponse. En effet, la signature isotopique en ^{13}C et ^{15}N d'un tissu peut permettre de retracer la provenance des ressources alimentaires qui ont été utilisées pour sa synthèse (**Boîte 1.3**, Hobson 1995, Kelly 2000). Cette analyse pourrait se faire en deux temps : i) afin de savoir si les femelles s'alimentent une fois arrivées sur leur site de ponte, on peut comparer la signature isotopique en ^{13}C et ^{15}N d'échantillons de méduses collectés sur la plage de ponte avec celle du plasma des femelles prélevés à leur première ponte. En effet, le plasma présente un taux de renouvellement court (de l'ordre d'une semaine, Hobson & Clark 1993) ce qui nous permettrait de « remonter » à la période de temps où les femelles se sont peut-être nourries. ii) afin de déterminer si cet apport alimentaire éventuel a été utilisé lors de la synthèse des œufs,

on peut comparer la signature isotopique en ^{13}C et ^{15}N d'échantillons de méduses collectés sur la plage de ponte avec celles des différents constituants des œufs (**Boîte 1.3**, Hobson 2006, Warner *et al.* 2007, Sénéchal *et al.* 2011).

Ainsi, si la première analyse révèle que les signatures isotopiques des méduses et du plasma sont différentes, alors on pourra conclure que les femelles tortues luth ne s'alimentent pas à leur arrivée en Guyane. Si toutefois la première analyse révèle des signatures isotopiques similaires (*i.e.* les femelles se sont nourries), et si la deuxième analyse montre des différences entre les signatures isotopiques des méduses et des œufs, alors on pourra conclure que l'apport alimentaire supplémentaire acquis par les femelles avant de commencer leur saison de ponte n'a pas été utilisé pour produire les œufs, mais a été alloué vers la maintenance maternelle. Dans ce cas, les tortues luth de Guyane pourront être considérées comme de stricts reproducteurs sur capital. Des études similaires devraient être appliquées aux populations de tortues luth nidifiant à Ste Croix et Grenade (Myers & Hays 2006, Casey *et al.* 2010) où il a été suggéré que les femelles s'alimentent pendant la saison de ponte, pour pouvoir statuer sur la stratégie de reproduction sur capital au niveau de l'espèce *Dermochelys coriacea*.

5.2. Quantification de la dépense énergétique associée à la reproduction

Dans notre travail, nous avons exprimé l'effort de reproduction des femelles tortues luth en termes de performance de reproduction (en nombre de pontes/saison ou en taille ou masse des pontes/saison). Ces indices très informatifs n'indiquent cependant pas la quantité d'énergie que chaque femelle a dépensée dans la production de ses pontes (Anguiletta & Sears 2000). Pour compléter notre approche, il serait intéressant d'estimer la quantité d'énergie que les tortues luth allouent à leur reproduction. Plusieurs méthodes peuvent être appliquées : il est possible i) d'estimer la valeur énergétique de chaque ponte, basé sur des mesures de l'énergie brute des œufs par calorimétrie (McLean & Tobin 1987) ; ii) de déterminer la dépense énergétique des femelles entre deux pontes successives, soit en utilisant la technique de l'eau doublement marquée (Wallace *et al.* 2005), soit en utilisant l'accélération dynamique partielle des femelles enregistrée pendant leur voyage en mer entre deux pontes successives, grâce au déploiement d'accéléromètres (Enstipp *et al.* 2011 pour la validation de la technique, **Annexe 4**).

5.3. Détermination des zones de migration

Afin de préciser l'influence des conditions environnementales sur la reproduction des tortues luth, il est nécessaire d'identifier précisément les sites d'alimentation que les femelles ont exploités au cours de leur migration. Cela nécessite de réaliser le suivi des femelles tout au long de leur migration. Ce genre de suivi implique que les tortues soient équipées de systèmes de positionnement tels que les balises Argos. Toutefois, la durée de vie de ces instruments arrive rarement au terme d'une migration (*e.g.* 1/ 46 balises déployées, Shillinger *et al.* 2011). D'autres systèmes de géolocalisation sont disponibles, mais pour s'affranchir du problème lié à la durée de vie des batteries, ils ne communiquent pas les données enregistrées. Ces instruments doivent donc être récupérés pour avoir accès aux données. De plus, à cause de leur carapace non-écaillée, équiper les tortues luth se révèle être un exercice plus difficile que pour les autres espèces de tortues marines. Deux méthodes sont actuellement employées : la première consiste à revêtir la tortue d'un harnais auquel est attaché l'enregistreur (Eckert & Eckert 1986). Cependant, comme nous avons pu le voir, les tortues prennent considérablement du poids au cours de leur migration, et il a été montré que l'utilisation de ces harnais sur de longues périodes pouvait blesser les tortues (Troëng *et al.* 2006, Sherill-Mix & James 2008, Salinas *et al.* 2009) et diminuer leur capacité de nage (Fossette *et al.* 2008d). Une autre méthode a donc été développée, qui consiste à attacher l'enregistreur directement sur une des carènes de la carapace de la tortue (Fossette *et al.* 2008d, **Fig. 4.10**). Cette dernière méthode est maintenant la plus couramment utilisée, aussi bien sur de courtes durées, *i.e.* entre deux pontes (Byrne *et al.* 2009, Casey *et al.* 2010) que sur de plus longues durées, *i.e.* pour la migration (*e.g.* Fossette *et al.* 2008d, Byrne *et al.* 2009, Witt *et al.* 2011). Malheureusement, sur ces dernières études, aucune tortue n'a pu être suivie pendant l'intégralité de sa migration. En 2008, nous avons équipé d'enregistreur de positionnement par la technique de l'attachement direct 46 tortues luth venues pondre en Guyane. Seule une femelle est revenue trois ans plus tard avec un enregistreur malheureusement défectueux (**Fig. 4.10**). Les futures recherches devront donc arriver à améliorer les techniques d'attachement à long terme, ce qui nous permettra enfin d'ouvrir la « boîte noire » des migrations des tortues marines dans leur intégralité.



Figure 4.10. Tortue luth 0601-0D68 « Mirette » observée le 27 mai 2011 après avoir été équipée d'un GPS (sur le dos, insert) le 2 Juillet 2008.

Une méthode alternative indirecte est également envisageable : elle consiste à comparer la signature isotopique en ^{13}C et ^{15}N de méduses prélevées sur les sites d'alimentation connus des tortues luth (Fossette *et al.* 2010a, **Annexe 1**) avec celle d'échantillon sanguin de femelles nidifiant en Guyane. Cette fois, l'utilisation des hématies est recommandée puisque leur taux de renouvellement est de l'ordre de plusieurs mois (Hobson & Clark 1993).

5.4. Développement de modèles de dynamique de population intégratifs

Le développement de modèles prédictifs de la dynamique des populations est essentiel pour l'établissement de mesures de conservation adéquates des espèces menacées, comme les tortues marines. En effet, toutes les espèces de tortues marines sont inscrites sur la liste rouge de l'IUCN (*International Union for Conservation of the Nature* ; <http://www.iucnredlist.org/>), et à l'échelle mondiale, la tortue luth est considérée comme étant en danger critique d'extinction (IUCN 2002).

Les traits d'histoire de vie comme le sex-ratio, le taux de succès à l'éclosion, la vitesse de croissance, les taux de survie juvénile et adulte, et les traits liés à la reproduction doivent être

intégrés aux modèles de dynamique des populations pour améliorer leur robustesse et leur pouvoir prédictif. Il a été montré que les modèles intégrant une approche individu-centré permettent d'aborder les compromis d'histoire de vie et présentent un fort potentiel de prédiction des dynamiques de population (Feró *et al.* 2008). Cependant, concernant les tortues marines, l'ensemble de ces paramètres est encore peu connu, compte tenu que l'accessibilité aux animaux est principalement restreinte aux femelles sur leur site de ponte. Ainsi, à ce jour, les modèles de dynamique de population développés pour les tortues marines reposent sur les comptages des effectifs des femelles reproductrices (*e.g.* Spotila *et al.* 1996, Girondot *et al.* 2007). Plusieurs études se sont également intéressées aux fluctuations des effectifs de femelles reproductrices et/ou des fréquences de reproduction en fonction des conditions environnementales (*e.g.* Broderick *et al.* 2001, Solow *et al.* 2002, Saba *et al.* 2007, Wallace & Saba 2009, Reina *et al.* 2009, Saba *et al.* 2012, Thorson *et al.* 2012). Toutefois, à l'exception d'une étude intégrant la performance de reproduction (*i.e.* nombre de pontes/saison, Rivalan *et al.* 2005), aucune n'a intégré les caractéristiques individuelles des femelles reproductrices, telles que la condition corporelle ou le comportement en mer.

Nous avons récemment montré, chez la population de tortues olivâtres nidifiant en Guyane, que le maintien d'un comportement spécifique lors de la reproduction (*i.e.* synchronie de la reproduction) peut déterminer la dynamique d'une population (**Annexe 3**). Dans ce travail de thèse, nous avons de plus souligné l'influence de la masse corporelle des femelles (et de leur condition) et des variations environnementales à courte échelle de temps sur les performances de reproduction et les compromis associés à la reproduction des tortues luth. Ainsi, afin que les modèles de dynamique des populations des tortues marines soient plus performants, nous encourageons les futures études à intégrer les variations des traits d'histoire de vie de ces espèces issues d'analyses individu-centré combinant des approches biométrique, physiologique et comportementale.

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6. ARTICLES



**Pleated turtle escapes the box
– shape changes in *Dermochelys coriacea***

J Davenport, V Plot, J-Y Georges, TK Doyle & MC James (2011)

Journal of Experimental Biology, 214 : 3474-3479

RESEARCH ARTICLE

Pleated turtle escapes the box – shape changes in *Dermochelys coriacea*

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SUMMARY

Typical chelonians have a rigid carapace and plastron that form a box-like structure that constrains several aspects of their physiology and ecology. The leatherback sea turtle, *Dermochelys coriacea*, has a flexible bony carapace strengthened by seven longitudinal ridges, whereas the plastron is reduced to an elliptical outer bony structure, so that the ventrum has no bony support. Measurements of the shell were made on adult female leatherbacks studied on the feeding grounds of waters off Nova Scotia (NS) and on breeding beaches of French Guiana (FG) to examine whether foraging and/or breeding turtles alter carapace size and/or shape. NS turtles exhibited greater mass and girth for a given curved carapace length (CCL) than FG turtles. Girth:CCL ratios rose during the feeding season, indicating increased girth. Measurements were made of the direct (straight) and surface (curved) distances between the medial longitudinal ridge and first right-hand longitudinal ridge (at 50% CCL). In NS turtles, the ratio of straight to curved inter-ridge distances was significantly higher than in FG turtles, indicating distension of the upper surfaces of the NS turtles between the ridges. FG females laid 11 clutches in the breeding season; although CCL and curved carapace width remained stable, girth declined between each nesting episode, indicating loss of mass. Straight to curved inter-ridge distance ratios did not change significantly during the breeding season, indicating loss of dorsal blubber before the onset of breeding. The results demonstrate substantial alterations in size and shape of female *D. coriacea* over periods of weeks to months in response to alterations in nutritional and reproductive status.

Key words: leatherback turtle, feeding, shape change, girth.

INTRODUCTION

Chelonians arose 210–230 million years ago (MYA) during the late Triassic as heavily armoured terrestrial forms, though all turtle species alive at present (terrestrial as well as aquatic) are believed to have evolved from aquatic ancestors (Joyce and Gauthier, 2004). The basic chelonian body plan differs from the typical reptilian pattern in many features, especially in terms of reduced vertebral articulation, the presence of a rigid bony shell and the location of the girdles within the rib cage (Romer, 1956). The rigid shell, which is a novel structure amongst tetrapods (Gilbert et al., 2001), forms a solid box composed of two parts: a dorsal carapace and a ventral plastron. The carapace is formed from costal bones with fused ribs, neural bones with fused thoracic vertebrae, and marginal bones (Gaffney and Meylan, 1988; Zangerl, 1980). The plastron of turtles is primitively formed from one unpaired and eight paired ossification centres, elements of which have homologies with clavicles and interclavicles (Romer, 1956; Gilbert et al., 2001). The carapace and the plastron are joined at the lateral margin (shell bridge) and enclose the pectoral and pelvic girdles (see Romer, 1956; Burke, 1991).

The fusion of the rib cage and shell constrains several aspects of turtle biology. The viscera can only occupy a restricted volume, so, for example, the chelonian body plan complicates turtle breathing (Gans and Gaunt, 1969). On land and in water, turtles exclusively use their appendicular system in locomotion, because the trunk is effectively rigid, prohibiting lateral or vertical undulation. The shell restricts the range of limb movement (Zug, 1971). The retraction

of the forelimbs and the protraction of the hindlimbs are both restricted by the shell bridge.

The evolutionary radiation of turtles on land and water has resulted in a great variety of modifications of the basic shell shape [see Renous et al. (Renous et al., 2008) for a recent synthesis]. Zangerl (Zangerl, 1980) and Lapparent de Broin et al. (Lapparent de Broin et al., 1996) have noted that there is a general tendency in aquatic turtles towards an incomplete and reduced paedomorphic shell. However, in the great majority of turtles the constraining arrangements of bony carapace, plastron and shell bridge remain, even if they are much reduced and some flexibility is introduced (e.g. by incorporation of cartilaginous material, as in the trionychid softshell turtles).

The leatherback sea turtle, *Dermochelys coriacea* (Vandelli 1761), the sole living species of the Dermochelyidae, is a very unusual turtle. The Dermochelyidae diverged from other turtles 100–150 MYA. Other extant marine turtles (Cheloniidae) are not closely related, having all evolved in the middle Tertiary some 35–50 MYA (Zangerl, 1980). This remote relationship was confirmed by molecular studies (Bowen et al., 1993). The leatherback is by far the largest living turtle species, adult animals typically weighing approximately 400–500 kg. The heptagonal leatherback shell structure differs greatly from the basic chelonian pattern (Deraniyagala, 1936; Deraniyagala, 1939). The carapace consists of several thousand small ossicles of irregular shape, joined to form a flexible mosaic that collapses quickly after death, making palaeontological investigations difficult. Much of the

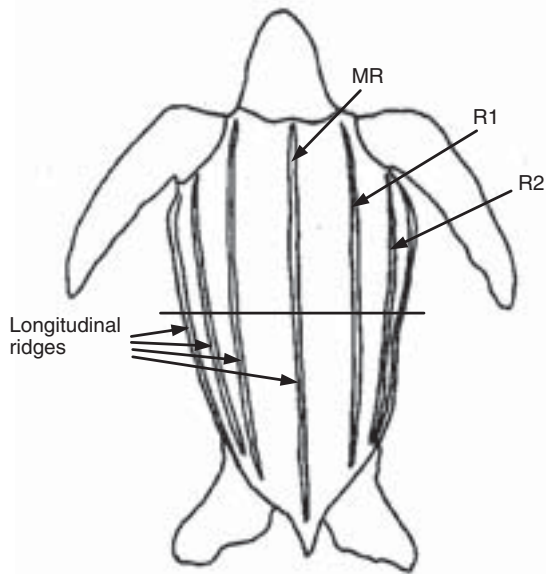


Fig. 1. Diagram of the dorsal surface of an adult leatherback turtle. MR, medial ridge; R1, R2, lateral ridges. Horizontal line indicates position of girth and inter-ridge measurements [at 50% curved carapace length (CCL)].

mosaic is extremely thin (3–4 mm) (Wood et al., 1996), but the carapace is strengthened by seven acute longitudinal ridges that run from the front of the carapace to its triangular rearmost portion (Fig. 1). Bony elements of the plastron of *D. coriacea* are centrally absent, being reduced to a thin elliptical bone (Boulenger, 1889; Wood et al., 1996; Wynken, 2001). Although the plastron is tough, relatively inflexible and contains dermal ossicles, there is no ventral axial bony protection for the viscera. This situation is quite unlike all other living turtles; Dermochelyidae appear to have progressively lost the central bony part of the plastron during their evolution as there is persuasive evidence that some fossil forms had plastral mosaics (Wood et al., 1996). All of the dorsal and ventral portions of the skeletal elements of the shell are covered by a thick, flexible, fibrous skin and lined with blubber. The ossicles of the carapace are lined ventrally with blubber. In a large male leatherback the skin was at least 1 cm thick and the blubber 2.8 cm thick in the plastral region, 2.5 cm thick in the carapacial region and approximately 5 cm thick at the bases of the four limbs (Davenport et al., 1990). Given the absence of bony elements in most of the plastron and a flexible carapace, the leatherback anatomy delivers a compliant structure already known to expand and compress in the ventral region during respiration (Lutcavage and Lutz, 1997). The ventrum has five reduced ridges, but these are compliant apart from ossified knobs (Boulenger, 1889).

The leatherback is also highly unusual in terms of its feeding ecology, biogeography and physiology. *Dermochelys coriacea* is an obligate feeder on gelatinous organisms, predominantly medusae, pyrosomas and siphonophores, throughout its life (den Hartog and van Nierop, 1984; Davenport and Balazs, 1991). Its diet is, therefore, of low calorific value for a carnivore (for discussion, see Doyle et al., 2007). This means that it has to eat very large quantities of food (Duron, 1978), from more than 100% body weight day⁻¹ in hatchlings (Lutcavage and Lutz, 1986), to at least 50% body weight day⁻¹ in adults (Davenport, 1998), far more than the volumes consumed by rigid-shelled cheloniid sea turtles. Bels et al. described how *D. coriacea* has a unique ability to simultaneously catch and swallow prey with a conveyor-like action, so that leatherbacks effectively

graze on concentrations of gelatinous organisms (Bels et al., 1998). Despite their low-calorie diet, *D. coriacea* grow very quickly (for discussion, see Jones et al., 2011), apparently reaching maturity at an age of approximately 16 years. Jones et al. suggest that assimilation efficiencies of gelatinous food may be very high, and contribute to this rapid growth (Jones et al., 2011).

The prey densities of leatherbacks are geographically very patchy and the turtles migrate annually over long distances between food-poor areas in the tropics and food-rich feeding areas in cool temperate coastal waters (e.g. James et al., 2005; Hays et al., 2006; Fossette et al., 2010a; Fossette et al., 2010b). Adult *D. coriacea* are well known to have core body temperatures elevated over ambient when in cool water (e.g. off Newfoundland and Nova Scotia) by virtue of large size (gigantothermy), blubber composition and countercurrent heat exchangers (Frair et al., 1972; Paladino et al., 1990; Davenport et al., 1990; James and Mrosovsky, 2004). Bostrom et al. have recently shown that even small juvenile turtles (16–37 kg) can sustain temperature gradients between the body and the external environment (Bostrom et al., 2010), so that *D. coriacea* is truly endothermic. There is good palaeoecological evidence that the capacity for Dermochelyidae to penetrate cool waters (and hence require endothermy/gigantothermy) is ancient (>40 MYA) (Albright et al., 2003).

It is already known that female leatherback turtles on feeding grounds off Nova Scotia are far heavier (by approximately 33%) for a given carapace length than females laying eggs on beaches in French Guiana (James et al., 2005; Georges and Fossette, 2006). Variations in body mass (condition) without apparent change in shell dimensions are well known from a variety of turtles, and are particularly associated with hibernation in terrestrial species (e.g. Hailey, 2000) and in female cheloniid sea turtles during the breeding season (e.g. Hays et al., 2002; Santos et al., 2010). Although leatherbacks in Canadian waters clearly carry much fat around the head, neck, pectoral and pelvic regions (Fig. 2), we hypothesised that the flexible shell of *D. coriacea* allows the animal to change its body size and shape in response to the demands of its biogeography and life history, whilst optimizing visceral function and locomotion. We would expect females to show a 'thin' appearance (flat/concave plastral surface, more prominent carapacial ridges) when anorexic and with depleted blubber and ovaries at the end of the breeding season. However, we would expect well-fed turtles on the feeding grounds to exhibit a more rotund appearance (convex plastral surface, less prominent carapacial ridges) to accommodate both blubber and large volumes of jellyfish. The aim of this study was to test this hypothesis by investigating a continuous population of leatherbacks known to feed off eastern Canada (Nova Scotia, Newfoundland) and breed over extensive parts of the Caribbean, including French Guiana (James et al., 2007).

MATERIALS AND METHODS

Leatherback turtles were captured at sea in the summers of 2007–2010 off Nova Scotia using methods as described by James et al. (James et al., 2007). Curved carapace length (CCL) and curved carapace width (CCW) were measured for putative female turtles with CCL >142 cm ($N=46$), which approximates the size range of nesting leatherbacks found on Western Atlantic beaches (Stewart et al., 2007). All turtles were categorized as male or female on the basis of tail length, which is consistently dimorphic (tails are longer in males) in animals >142 cm CCL; they were sexed by the same observer (M.C.J.). Data for males are not considered in this paper as none are available for males in the breeding areas. When possible, other indices of body condition were collected, including girth at



Fig. 2. Above: Nova Scotian female leatherback (courtesy of Canadian Sea Turtle Network, 2010; with permission), demonstrating deposition of blubber in neck, pectoral and pelvic areas. Note the smooth surface between longitudinal ridges. Below: female turtle on a breeding beach in French Guiana (courtesy of V. Plot, with permission). Note lack of fat rolls on neck and at bases of flippers. Note also the marked indentation in skin between longitudinal ridges of the carapace.

50% CCL ($N=31$; Fig. 1) and mass ($N=15$). In some cases ($N=22$) it was also possible to measure the distance between the medial longitudinal ridge (MR) and the nearest lateral ridges (R1) on both sides, both directly (straight) and along the dorsal surface (curved) at the 50% CCL level (Figs 1, 3). All measurements were made to the nearest millimeter with inextensible metal tapes. Measurement of R1–R2 (Fig. 1) was not feasible at sea.

One hundred and eighty-two female turtles were investigated during the 2005 breeding season at Awala Yalimapo beach, French Guiana (5.7°N , 53.9°W), as described by Georges and Fossette (Georges and Fossette, 2006). CCL, CCW and girth were measured (to 0.5 cm) for all turtles after they had laid the first clutch of the breeding season. During the 2010 breeding season, 33 females were remeasured on the same beach for these same variables after they had laid each clutch (i.e. repeated measures). As clutch number was very variable (≤ 11) amongst females, this meant that the number of turtles measured declined during the breeding season (in addition, it was sometimes not possible to measure a female after oviposition). In the case of those 33 animals it was also possible to measure the distance between MR and R1, and between R1 and R2 on both sides, both directly (straight) and along the dorsal surface (curved) at the 50% CCL level (Figs 1, 3).

RESULTS

Comparisons of length (CCL), girth and girth:CCL ratios between turtles from Nova Scotia and French Guiana

Data are summarized in Table 1. Analysis by one-way ANOVA was used (except in the case of girth comparisons), preceded by a normality test (Anderson–Darling) plus F -tests and Levene's tests for homogeneity of variance. Data sets for CCL, and girth:CCL ratio were normal and homogenous. The girth data set for French Guiana (FG) was non-normal, so FG and Nova Scotia (NS) girths were compared using a nonparametric test (Kruskal–Wallis). ANOVA

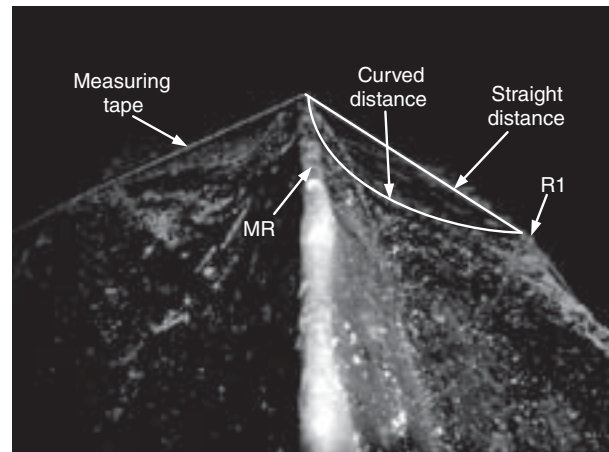


Fig. 3. Photograph of the dorsal surface of a female leatherback turtle taken at night (from the rear) whilst nesting in French Guiana (courtesy of V. Plot, with permission). MR, medial ridge, R1, lateral ridge nearest to MR. White lines have been added to indicate curved and straight inter-ridge distances measured in this study.

showed that mean FG CCL was significantly greater (by 4.7 cm; 3.03%) than mean NS CCL ($F=24.9$, $P=0.004$). We would therefore expect FG girth to be greater than NS girth from known mass–length relationships (Georges and Fossette, 2006). However, the mean NS girth was significantly greater (by 15.3 cm; 7.69%) than mean FG girth (a Kruskal–Wallis test of the median girths of the two samples revealed a significant difference; $H=17.7$, $P<0.0005$). NS turtles had a much greater girth for a given CCL than FG turtles.

Changes in girth:CCL ratio during presence in Nova Scotia waters

It is not logistically feasible to follow the growth of individual turtles when on the northern feeding grounds. Turtles sometimes arrive in June, but most are present in July and August. The relationship between the girth:CCL ratio and day-of-year (ordinal date) of capture and measurement during 2007–2009 is presented in Fig. 4. Simple linear regression analysis demonstrated a significant positive relationship ($r^2=0.306$ $P=0.001$), with the ratio rising with elapsed time during the year. This indicates that the females became relatively more rotund (greater girth for a given CCL) between arriving on the feeding grounds and departing.

Comparison of inter-ridge shapes in turtles from Nova Scotia and French Guiana

There was no statistically significant difference between MR–R1 distances (see Fig. 1 for definitions) on the left and right for either

Table 1. Mean (\pm s.d.) curved carapace length (CCL) and body girth (measured at 50% CCL) in female leatherback turtles sampled in waters off Nova Scotia, Canada, and studied on breeding beaches in French Guiana

	French Guiana ($N=182$)	Nova Scotia ($N=29$)
CCL	159.3 \pm 6.83	152.4 \pm 7.56
Girth	198.9 \pm 14.04	214.2 \pm 12.58
Girth:CCL	1.249 \pm 0.074	1.386 \pm 0.086

All measurements are in centimeters. Values of the girth:CCL ratio are also given for both samples.

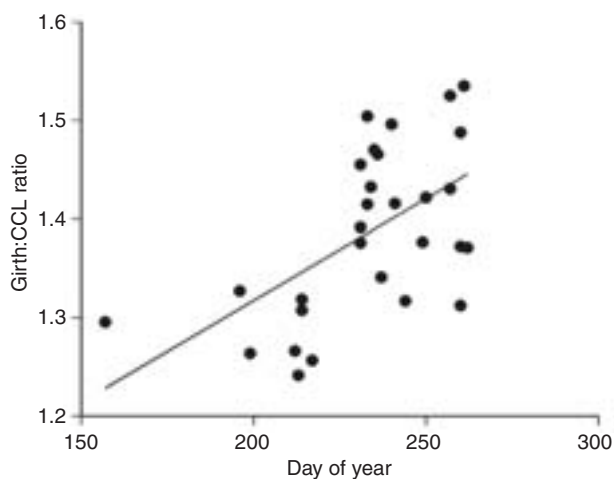


Fig. 4. Relationship between the girth:CCL ratio and day-of-year (ordinal day) of capture or measurement in female leatherbacks collected in Nova Scotia waters ($N=29$). Solid line represents linear regression ($r^2=0.306$, $P=0.001$) of data. $\text{Girth:CCL ratio} = 0.904 + 0.0021 \times \text{day-of-year}$.

NS or FG turtles (ANOVA, $P>0.05$). Accordingly, all analyses were carried out on data for the right-hand side of turtles. For both groups of turtles, $(\text{MR-R1 straight})/(\text{MR-R1 curved})$ was computed. This straight:curved ratio is close to 1 if there is little difference between the two measurements, but is lower if there is a deeper curve. Ratio data (NS: $N=22$, mean \pm s.d. straight:curved ratio = 0.9833 ± 0.008 ; FG: $N=33$, mean straight:curved ratio = 0.9635 ± 0.016) were normal (Anderson–Darling test: NS, $P=0.081$; FG, $P=0.894$), but variances were not homogenous (F -test, Levene's test) because NS data were much less variable than the FG data. Accordingly, a non-parametric Kruskal–Wallis test was used to compare median straight:curved ratios (NS, 0.9841; FG, 0.9652). There was a significant difference between the medians ($H=20.9$, $P<0.0005$). The ratio was significantly higher for NS females, indicating that these females had significantly less indented upper surfaces than FG nesting females.

Changes in female CCL, CCW and girth during the breeding season in French Guiana

Individual leatherback females laid several (≤ 11) egg clutches at regular intervals (~ 10 days) during a single breeding season on beaches in French Guiana. Because of repeated irregular measurements we used a linear mixed-effects model (LME; using R 2.10.1 for Windows; www.r-project.org) with the turtles' ID as a random factor to take into account the pseudo-replication within the data set. Measurements of females up to the eighth clutch were considered in these analyses, as eight is the average number of clutches laid by leatherback females in the French Guiana population. The results showed that females' CCL and CCW did not change throughout the breeding season (LME, $P=0.2969$ and $P=0.2846$, respectively, $N=33$) whereas girth decreased significantly (LME, $P<0.001$; coefficient $a=-1.6$, $N=33$). Fig. 5 shows that CCL and CCW of such females were stable, but girth declined considerably with clutch number. For 14 females, the mean change in measurement (cm) of CCL, CCW and girth measured after laying clutch 1 and clutch 8 were -0.79 ± 0.80 , $+0.07 \pm 1.21$ and -11.36 ± 3.91 , respectively, again confirming the stability of CCL and CCW, but changeable girth.

Leatherback shape changes

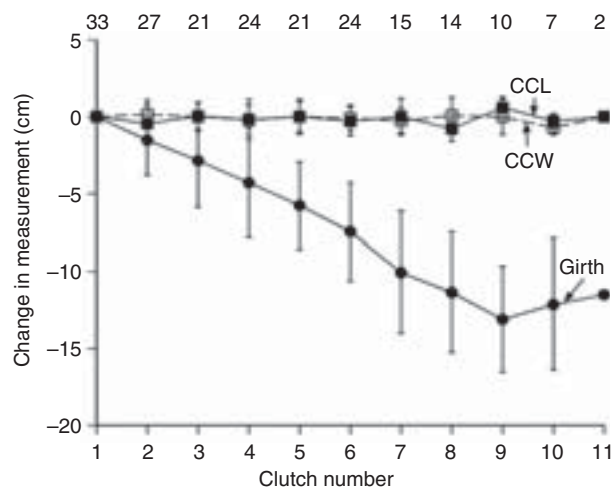


Fig. 5. Changes in measurement of leatherback turtles with respect to measurement after laying the first egg clutch of the breeding season in French Guiana. CCW, curved carapace width; girth, circumference of animal at 50% of CCL. Data are means \pm s.d. Numerals above the graph correspond to the number of turtles measured after each clutch laying.

Changes in female inter-ridge shape during the breeding season in French Guiana

LME was also used as described above, but was preceded by a Box–Cox transformation in order to achieve normality of the ridge ratio data. The model showed that the ridge ratio did not change significantly (LME, $P=0.37$, $N=33$). There was no significant change in shape of the upper surface of the carapace during the breeding season.

DISCUSSION

This study has necessarily been limited to female leatherback turtles as males are inaccessible on the tropical feeding grounds. There is no anatomical reason why males should not show similar alterations in body shape, but by analogy with recent studies on loggerhead turtles (*Caretta caretta*) by Hays et al. (Hays et al., 2010), their magnitude and timing are likely to be different, because it is probable that breeding frequencies and durations of residence of breeding and feeding grounds will differ between the sexes.

From our study it is evident that the shape of the shell of female *D. coriacea* can change in two ways. First, the girth can alter, both between low latitude Caribbean breeding beaches and the feeding grounds off Nova Scotia, and during the feeding and breeding seasons themselves. The girth increases on the feeding grounds and decreases by the beginning of the breeding season, presumably as a result of blubber loss caused by a combination of the costs of southward migration and part of the investment in reproduction (which will continue during the breeding season). The girth decreases still further during the breeding season as each clutch of eggs is laid. Roughly speaking, for a turtle of 150 cm the difference in girth between a well-fed animal off Nova Scotia and a female at the end of the breeding season will be approximately 30 cm (ca. 15% of girth).

Second, the shape of the dorsal surface is changeable, as hypothesised. Well-fed animals off Nova Scotia have smoother dorsal surfaces, with less prominent longitudinal ridges than nesting females on the beaches of French Guiana (Fig. 2). This presumably reflects the deposition of blubber beneath the dorsal skin (which stretches) evident in dissections of stranded and drowned animals

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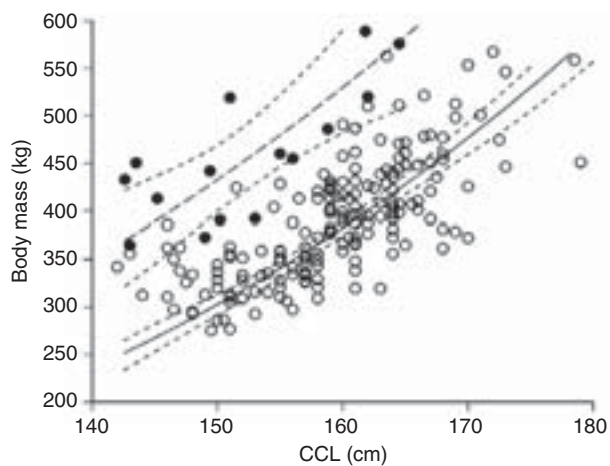


Fig. 6. Relationships between CCL and body mass for female leatherback turtles [extracted from James et al. (James et al., 2005), with additional data from the present study]. Open circles represent French Guiana (FG) females ($N=182$), solid circles represent Nova Scotia (NS) females ($N=15$). The solid curve represents the reduced major axis regression of FG female data [$\log(\text{body mass})=3.631\log(\text{CCL})-5.420$; $r^2=0.512$, $P<0.0001$]. The 95% confidence limits for the slope (3.631) are 3.251 and 4.060, so growth is positively allometric (i.e. turtles become relatively heavier as they grow) not isometric. The heavy dashed curve represents the reduced major axis regression of NS female data [$\log(\text{body mass})=3.133\log(\text{CCL})-4.182$; $r^2=0.547$, $P=0.0016$]. NS data are few and the confidence limits for the slope (3.133) are wide (2.223 and 4.157). Upper and lower 95% confidence intervals are indicated by light dashed curves.

at high latitude (e.g. Davenport et al., 1990). Interestingly, the measured shape of the dorsal surface does not change during the breeding season itself, even though the turtle may lay ≤ 11 clutches and show marked reductions in girth. This suggests that the blubber beneath the dorsal skin and carapace is largely exhausted by the beginning of the breeding season. However, these statistical conclusions contrast with field observations where some females appear to have more prominent carapace ridges, and a more concave carapace at the end of the breeding season, up to a stage where their sacral vertebrae may be visible underneath the skin. The non-statistical significance in the change of the ridge ratio may reflect the position of the measurements (mid CCL).

Fig. 6 shows data for the length–body mass relationships of NS and FG females. For FG females it may be calculated that a turtle with a CCL of approximately 150 cm will have a body mass of approximately 300 kg. From the data presented by James et al. (James et al., 2005) we know that such a female will weigh approximately 400 kg when in waters off Nova Scotia. A female turtle of CCL 150 cm has a surface shell area of approximately 3 m^2 [estimated from a leatherback drawing (Fig. 1) scaled to a carapace length of 150 cm]. If we assume an average blubber thickness when in northern waters of approximately 3 cm (cf. Davenport et al., 1990), this translates into a volume of some 90 l of blubber (roughly 72 kg, assuming a fat density of 0.8 g ml^{-1}) lining the shell and surrounding the viscera. There are no data for blubber thickness in nesting females, but even if all blubber (i.e. 72 kg) is used up during migration and reproduction, it can only explain approximately 72% of the discrepancy in mass (100 kg) between NS and FG females. The remainder (approximately 28 kg) is presumably stored in the obvious rolls of fat seen around the neck, pectoral and pelvic regions of females seen on the northern feeding grounds (Fig. 2). These

approximate calculations suggest that the distended shell accommodates approximately three-quarters of the accumulated fat. It is already well known that female *D. coriacea* demonstrate the highest maternal investment of all living reptiles (for reviews, see Wallace et al., 2006; Wallace et al., 2007). They lay multiple (normally seven to eight, but <11) large egg clutches (approximately 65 eggs per clutch) of the largest eggs (80–90 g each and approximately 53 mm diameter) of any sea turtle and do so every 2–4 years for decadal periods (Spotila et al., 1996). From the data of Miller (Miller, 1997) and Reina et al. (Reina et al., 2002b) it can be estimated that a female may lay approximately 35 kg of eggs (equivalent to approximately 371 volume) per breeding season. Unlike all other turtles, leatherback females also lay very variable numbers of shelled albumen gobs (formerly known as yolkless eggs) that have an uncertain function (Wallace et al., 2007). Hence it is probable that a female will deposit approximately 40 kg (ca. 42 l) of material in a single breeding season. Although much of the deposited volume will consist of water (replaceable by drinking seawater, so involving salt regulation energetic costs), it indicates the scale of maternal reproductive investment involved in this species. Feeding opportunities during the breeding season are limited (but see Fossette et al., 2008; Casey et al., 2010), so much of the decline in girth between each clutch will presumably reflect loss of blubber as a result of fasting, as well as (indirectly) a decline in ovary size.

There is no reason to suppose that the anorexic appearance of females at the end of the nesting season (Fig. 2) is due to dehydration. Leatherback sea turtles have extremely large salt glands that occupy a large proportion of the skull volume (e.g. Wyneken, 2001; Davenport et al., 2009) and produce copious, highly concentrated secretions; Reina et al. (Reina et al., 2002a) demonstrated that even desiccated hatchling leatherbacks can drink seawater to recover water balance within 12 h. A 500 kg female that has just laid a single clutch of eggs will have little difficulty in drinking (and desalting) approximately 4–5 l ($<1\%$ body volume) of seawater to compensate for lost water. Moreover, several studies have presented evidence that females drink during inter-nesting intervals (Myers and Hays, 2006; Fossette et al., 2008; Casey et al., 2010), thus allowing females to incorporate water into the next clutch.

It is evident that leatherback life history and foraging strategy are only compatible with a structure that allows substantial alterations in size and shape over relatively short periods (weeks to months). An effectively pleated upper surface, combined with a ventral body wall that can shrink or distend, permit the great fecundity of this wide-ranging species and the long migration distances between high latitude foraging and low latitude breeding grounds. Some hard-shelled turtles (e.g. the green turtle *Chelonia mydas*) can show distension of the plastron when well fed (Heithaus et al., 2007), whereas numerous aquatic chelonian species exhibit reduced bony elements of the shell and enhanced flexibility (Zangerl, 1980; Lapparent de Broin et al., 1996). However, the considerable capacity in leatherbacks for distension of both carapace and plastron is unusual. It also needs to be realized that a compliant body wall additionally permits intake of huge meals and is a factor in the species' remarkable diving ability. Several factors have therefore driven the evolution of the capacity for *D. coriacea* to escape many of the constraints of the ancestral box.

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**Leatherback turtles are capital breeders:
Morphometric and physiological evidences
from longitudinal monitoring**

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Physiological and Biochemical Zoology (accepté avec révisions)

Abstract

Organisms compensate for reproduction costs through two major strategies: *capital breeders* store body reserves prior to reproduction and do not feed during the breeding season, whereas *income breeders* adjust their food intake depending on concurrent reproductive needs. Sea turtles are commonly considered capital breeders. Yet recent biometric and behavioral studies have suggested that sea turtles may in fact feed during reproduction. We tested this hypothesis in the leatherback turtle *Dermochelys coriacea* nesting in French Guiana. Our study is based on the innovative use of longitudinal monitoring for morphological (body size, body mass and body condition) and physiological (plasma glucose, triacylglycerides, urea, calcium and hematocrit) measurements in 35 females throughout the 2006 nesting season. During their 71-day nesting period, leatherbacks lost 46.8 ± 2.6 kg (mean \pm SE; i.e., $\sim 11\%$ of their initial body mass of 409.0 ± 8.9 kg). Simultaneously, a significant decrease in plasma concentrations of glucose, triacylglycerides and urea was observed throughout the nesting season, following typical patterns reported in other long-fasting animals relying on lipid body stores. At the end of the nesting season, the inter-individual variability in plasma concentrations was very low, which may characterise some minimum thresholds associated with the end of reproduction. We also identified a minimum necessary threshold for female body condition at the onset of reproduction; the body condition of any females beginning the nesting period below this threshold depressed dramatically. This study provides evidence that leatherbacks nesting in French Guiana are capital breeders, and further highlights the mechanisms that prevent this multiparous reptile from jeopardizing its own body condition whilst not feeding during reproduction.

Introduction

Organisms exploit their environment to ensure survival, maintenance, growth and reproduction, and ultimately to maximize their fitness (Stearns 1992). However, the temporal and spatial fluctuations in resources that are inherent to a heterogeneous natural environment can entail variable periods of food deprivation for organisms (Mrosovsky & Sherry 1980). Organisms thus face trade-offs between competing life functions, and compensate for this by adopting adaptative strategies at different levels (i.e., physiological, morphological, behavioural, and ecological) to ensure an optimal balance between energy acquisition and expenditure (Le Maho 2002).

Reproduction is generally considered to be an energetically highly costly life function. Organisms compensate for reproduction expenses by increasing trophic resource quantities through two different strategies: *Capital breeders* store large quantities of body reserves prior to reproduction then cease feeding during the reproductive episode, and *income breeders* adjust food intake during reproduction (Drent and Daan 1980; Jönsson 1997). In the wild, some species complement previously-stored body reserves by feeding during the reproductive season. This type of intermediate strategy has been suggested in mammals (e.g., Wheatley et al. 2008), birds (e.g., Drent and Daan 1980; Sénéchal et al. 2011), and reptiles (e.g., Lourdais et al. 2002, Warner et al. 2008, Fossette et al. 2008a).

Sea turtles are commonly considered capital breeders (*sensus* Drent and Daan 1980), with females relying on body reserves stored during the preceding migration and ceasing to feed during reproduction (Miller, 1997). Recent morphometric (body mass change) and behavioral (diving and mouth opening patterns, oesophageal temperature) studies have however contradicted this assertion in four of the seven sea turtle species. Opportunistic feeding during the reproductive season has already been suggested in green turtles (*Chelonia mydas*; Hochscheid et al. 1999), hawksbill turtles (*Eretmochelys imbricata*; Santos et al. 2010),

loggerhead turtles (*Caretta caretta*; Schoefield et al. 2006) and leatherback turtles (*Dermochelys coriacea*; Southwood et al. 2005, Fossette et al. 2008a, Casey et al. 2010).

At the physiological level, organisms adapt to food resource deprivation by using the *supply-side strategy* (McCue 2007a). The *supply-side strategy* results in successive specific metabolic pathways of body reserve mobilization. It has been extensively described in endotherms (birds, e.g., Groscolas 1986; Cherel et al. 1988; Robin et al. 1998; mammals, e.g., Arnould and Rawlins 2001; Guinet et al. 2004), and consists of three consecutive phases (Cherel et al. 1988). At the onset of the fast (phase I), postprandial animals enter a period of adaptation characterised by the exhaustion of glycogen stores and the progressive mobilization of lipid stores. As fasting continues (phase II), fat stores are preferentially mobilized and low use is made of body proteins. Beyond a critical level of fat store depletion, long-fasting animals enter a critical phase (phase III) where body proteins are increasingly catabolised. Recent studies on fasting ectotherms report similar patterns, with snakes chiefly relying on lipid stores while sparing proteins (McCue 2007a; 2007b; 2008). Investigating metabolic pathways during the reproduction period could therefore be a valid new approach to assessing the reproductive strategy (*i.e.*, income vs capital strategy) used by sea turtles.

Reproduction in sea turtles is energetically costly since adult females come ashore regularly during the nesting season (that lasts several weeks) to lay successive clutches of several dozens of eggs, with some inter-specific differences (*i.e.*, ranging from 50 eggs per clutch in the flatback turtle *Natator depressus* to 130 in the hawksbill turtles; Miller 1997). This high reproductive output most likely relies exclusively on previously-stored maternal body reserves (Miller 1997). Surprisingly, few studies have investigated the metabolic adjustments in nesting sea turtles, probably due to constraints in performing longitudinal monitoring in the field (Hamann et al. 2002; Honarvar et al. 2011). Only a few studies on captive sea turtles have reported changes in plasma metabolites during periods of food deprivation (marginally

shorter than during natural fasting in the wild; see Bonnet 1979; Moon et al. 1999). Hamann et al. (2002) showed patterns of plasma triacylglycerides and total proteins during the nesting season in green turtles and concluded that nesting females chiefly rely on lipid stores and may shift to protein catabolism at the end of the season. In the leatherback, Honarvar et al. (2011) reported a decrease in plasma proteins as the season proceeds. Although some recent studies have reported plasma metabolite levels in leatherbacks when nesting or on foraging sites, these results were not interpreted in terms of fasting physiology, since they were based on transversal monitoring (e.g., Innis et al. 2010; Harris et al. 2011).

The leatherback turtle is the largest sea turtle species: the average adult leatherback female weighs between 250 and 400 kg, depending on the nesting population (see Georges and Fossette 2006). This species shows the highest reproductive effort among sea turtles. Females lay an average of 6 clutches per season, with differences between nesting sites (Miller 1997) and between individuals (from 2 to 14 clutches per season; Eckert et al. 2012). During a nesting season that may last up to 3 months, leatherbacks lay successive clutches about 10 days apart. This period is defined as the internesting interval (Miller 1997).

In French Guiana, where nesting leatherbacks are larger and heavier (Georges & Fossette 2006) and lay more clutches (Girondot & Fretey 1996) compared to other sites, females have been shown to disperse actively and extensively over the continental shelf during internesting intervals (Fossette et al. 2007; Georges et al. 2007). Clear patterns of mouth opening at depth on the Guianese continental shelf have also been reported (Fossette et al. 2008a). In addition, the occurrence of jellyfish - the main prey of leatherbacks - has been reported in the vicinity of these nesting beaches (Fossette et al. 2009). These findings led to the hypothesis that leatherbacks in French Guiana may opportunistically feed during the nesting season. Similar hypotheses based on body mass change (St Croix, US Virgin Island; Eckert et al. 1989), mouth-opening patterns (Grenada, Western Indies; Myers and Hays 2006) or gut temperature

records (St Croix; Southwood et al. 2005, Casey et al. 2010) have been proposed for other leatherback nesting populations in the Atlantic ocean. However, these hypotheses are based on inference without any information on the actual physiological status of the study individuals. Here we aimed to test whether or not leatherback turtles feed during the nesting season in French Guiana using the longitudinal monitoring of morphometric (body length, width and mass) and physiological (glucose, triacylglycerides, urea, calcium and hematocrit) parameters as indicators of body condition and nutritional status in 35 leatherback females throughout their nesting season.

Materials and Methods

This project respected the legal requirements of the country in which the work was carried out and followed all institutional guidelines. This study was carried out under CNRS-IPHC institutional license (B67 482 18 delivered by Departmental Direction of the Veterinary Services, Strasbourg, France; and Police Prefecture of Bas Rhin) and under individual licences to JYG (67-220 delivered by the Departmental Direction of the Veterinary Services, Strasbourg, France; and the Police Prefecture of Bas-Rhin).

Study site

This study was conducted throughout the entire 2006 nesting season (March-July) at one of the world's largest nesting site for leatherback turtles (Fossette et al. 2008b): Awala Yalimapo beach (5.7°N, 53.9° W), French Guiana, South America. Monitoring programmes on this beach have been running since the late 1970's for individual identification, using external metal tags (Monel tags, National Band and Tags), and then internal passive integrated transponder tags (PIT, Trovan Euroid) since 1995 (Fossette et al. 2008b). All individuals

considered in the present study were marked remigrants (i.e., females tagged as nesters during previous seasons, see Fossette et al. 2008b).

Field protocol

Between March 15 and July 21, 2006, a 4 km-long stretch of the beach where most nesting events historically occur (Fossette et al. 2008b) was patrolled every night from 06:00 pm to 07:00 am. All remigrant turtles encountered during these patrols were individually identified by their PIT tag. Our monitoring consisted of (i) recording identity, date of oviposition and body morphometrics, (ii) counting yolked eggs, weighing the entire clutch at the first observed oviposition, and sampling three yolked eggs from each clutch to estimate clutch mass, (iii) sampling blood during oviposition and (iv) weighing females after oviposition when they were returning to the sea (details below). This sequence of manipulations ensured minimal disturbance, as confirmed by direct observations of all manipulated turtles completing their oviposition and returning to lay subsequent clutches. In total 35 females were monitored with complete measurements and blood samples for almost all successive clutches during their entire nesting season.

The longitudinal monitoring was carried out as follows: (i) During each observed nesting event, morphometric measurements (Standard Curvilinear Carapace Length SCCL, Standard Curvilinear Carapace Width SCCW) were taken using a flexible measuring tape (± 0.5 cm, following Georges and Fossette 2006). (ii) At the first observed clutch of each turtle, before the first egg was laid, a fabric bag with its base closed by a knotted lace was fitted in the nest chamber. During oviposition all eggs were collected in this tissue bag and yolked eggs were simultaneously counted using a hand tally counter. Three yolked eggs were collected by hand during egg counting. Once the last egg was laid and before the female started covering its nest, the bag was removed from the nest. A bucket was inserted in the nest chamber and the

female's hind flippers were held by hand out of reach of the sand to prevent the nest chamber from being filled with sand during the clutch weighing. Meanwhile, the clutch was weighed in the bag (± 0.05 kg) using a hand-held spring scale. After clutch weighing (approximately 20 seconds), the bucket was removed and the bag was replaced into the nest chamber. The lace was untied to open the bottom of the bag, which was then gently removed from the nest chamber. The eggs were hence red deposited into the nest chamber in a similar order to the one they had been laid in. The flippers were released, allowing the turtle to cover the nest. Due to the heavy logistical needs of this protocol, only the first observed clutch of each turtle was weighed in this way. The mass of subsequent clutches was estimated by calculating the mean mass of the 3 yolked eggs collected during egg counting (± 0.1 g), then multiplying this value by clutch size. This estimation method for individual clutch mass was validated for the first observed clutches, as no significant differences were found between clutch mass weighed with the bag and clutch mass estimated from the 3 collected eggs (7.0 ± 0.3 kg vs 6.7 ± 0.3 kg respectively; t paired test, $P=0.48$, $t=-0.70$, $n=33$ clutches). (iii) During each observed oviposition, a 6-ml blood sample was collected from the femoral rete system, using a syringe. The blood was immediately transferred into heparinised polypropylene microtubes and placed in a refrigerated cool box until the patrol was finished. Hematocrit measurement was then carried out (maximum 4 hours after sampling) using one capillary tube of whole blood, and blood samples were centrifuged to separate plasma and blood cells. Samples were frozen (-20°C) until they could be analyzed at the IPHC, Strasbourg, France. (iv) After oviposition, turtles were weighed (± 0.2 kg) when returning to the sea using a customised harness and an electronic spring scale fixed to a 4.5-m high carbon fibre tripod equipped with a hoist (see details in Georges and Fossette 2006).

Reproductive effort

For each individual we defined the ‘observed nesting period’ as the period between the first and the last observed clutches. Despite our exhaustive night patrols, some clutches were not observed because leatherbacks may nest outside the hours of our patrol schedule. Therefore, we calculated the Estimated Clutch Frequency (ECF) for each female following Frazer and Richardson (1985): The ECF is the total number of clutches that a turtle is believed to have deposited during its nesting season, taking into account the intermediate non-observed clutches (based on the mean inter-nesting duration of 10 days in leatherbacks, Girondot and Fretey 1996). This also permitted the calculation of cumulative clutch size and cumulative clutch mass for each female by multiplying its ECF by the mean clutch size and by the mean clutch mass of its observed clutches, respectively. We also defined the Level of Reproductive Effort (LRE), adapted from Hamann et al. (2002), as an index of the progress of the season: For a given clutch (x), LRE was calculated as: $LRE_{\text{at clutch } x} = (x/ECF) * 100$. LRE provides a better proxy of the relative reproductive effort through time compared to clutch rank. For instance, for one turtle laying 5 clutches (ECF=5) and a second turtle laying 10 clutches (ECF=10), LRE for a given clutch (e.g., the 4th clutch) will be twice as high for the turtle with lowest ECF (LRE = 80%) in comparison to the turtle with highest ECF (LRE = 40%).

Maternal body condition index

An index of maternal body condition (BCI) was calculated for each individual at every observed clutch as an indicator of individual health (Peig and Green 2009). As variation in body mass can be associated with differences in nutritional status as well as structural size, differences between body mass and structural size thus constitute a good index of nutritional state (Schulte-Hostedde et al. 2005). BCI was calculated following Saraux et al. (2011). First, a structural size index (SSI) was calculated using body length and body width, both good descriptors of sea turtles structural size (e.g., Georges & Fossette 2006). As SCCL and SCCW

were correlated (linear regression, $P < 0.001$, $R^2 = 0.41$), we used a principal component analysis to establish the SSI. The first principal component between these two parameters explained 82% of the variation. Secondly, the body condition was defined as the residuals of a regression of body mass on SSI (Schulte-Hostedde et al. 2005, Saraux et al. 2011). Since maternal BCI was calculated for each individual at every observed clutch throughout the observed nesting period, we used a Linear Mixed Effect models (LME) with the identity of the turtle as a random factor.

Plasma parameter concentrations

Plasma metabolites (glucose, triacylglycerides (TG) and uric acid or urea) are associated with specific metabolic pathways involved in the mobilization of successive body reserves (Robin et al. 1998) and are commonly used as indicators of the physiological and nutritional status in animals. In turtles, urea is described as the main product of protein catabolism instead of the uric acid reported in birds (Dessauer 1970, Bonnet 1979). Furthermore, the fact that in sea turtles urea does not play the osmoregulatory role reported in other marine vertebrates (Lutz, 1997, Acher et al., 1999) gives assurance that plasma urea concentrations are not biased by any other physiological processes than protein metabolism. Urea was thus used as an indicator of protein catabolism.

Plasma concentrations of metabolites were measured using 10 μL of undiluted plasma with commercial enzymatic colorimetric kits (glucose: Glucose-RTU, 61 269/61 270; TG: TG-PAP 150, 61 236; urea: Urea-Kit S180, 61 912/61 913; BioMérieux). Since calcium may be associated with egg production, plasma concentrations of calcium were also measured using 6 μL of undiluted plasma with commercial colorimetric method kits (Ca-Kit 61041, Thermo Fischer Scientific).

Statistical analyses

Results are given as means \pm Standard Error [min, max; n]. Statistical tests were processed with R software (2.10.1). Normality was checked before each test using the Shapiro-Wilk test. Tests for correlation were run with linear regression or the Spearman correlation test. Changes in morphometric measurements, body condition, physiological parameters and clutch mass throughout the observed nesting period were investigated using Linear Mixed Effect models (LME) when residuals fitted with normal distribution and Generalized Estimating Equation model (GEE) was used when residuals did not fit with normal distribution. This allows controlling for pseudo-replication by including individual identity as a random factor. Multiple comparisons were then applied with a Tukey's post-hoc test (after LME) or Wilcoxon paired test (after GEE). Potential changes in reproductive output, body mass, body condition and physiological parameters throughout the observed nesting period were investigated, considering LRE to be the time scale.

Results

Morphometrics and blood values at first observed clutch

At the first observed clutch, the 35 nesting females were on average 159.0 ± 1.5 cm long (SCCL) [141.5, 172.0 cm], 116.0 ± 1.0 cm wide (SCCW) [107.5, 125.0 cm] and weighed 409.0 ± 8.9 kg [289.6, 508.0 kg], corresponding to a mean maternal body condition index (BCI) of 25.1 ± 1.8 [4.7, 45.3]. At that time, mean physiological parameters values for the 35 females were as follows: hematocrit: $40.5 \pm 1.0\%$ [26.1, 57.0%], glucose: 12.46 ± 0.64 mmol.L⁻¹ [8.66, 24.00 mmol.L⁻¹], triacylglycerides (TG): 12.89 ± 0.56 mmol/L⁻¹ [2.10, 19.60 mmol.L⁻¹], urea: 1.14 ± 0.08 mmol.L⁻¹ [0.33, 2.13 mmol.L⁻¹] and calcium 3.25 ± 0.18 mmol.L⁻¹ [1.40, 5.81 mmol.L⁻¹].

At the first observed clutch, there were no significant relationships between maternal BCI and plasma concentrations of glucose, TG and urea ($P=0.32$, $P=0.48$ and $P=0.23$, respectively). We did however find a positive trend between maternal BCI and calcium ($P=0.067$, $R^2=0.10$) and a significant positive relationship between maternal BCI and hematocrit ($P=0.01$, $R^2=0.18$). Statistical significances were similar when maternal body mass was considered instead of BCI.

Reproductive parameters, morphometrics and blood values

The observed nesting period of the 35 study individuals (i.e. the time elapsed between the first and the last observed clutches) lasted on average 71.2 ± 2.6 d [40, 98 d; $n=35$ females], with a mean inter-nesting interval of 9.9 ± 0.1 d [8.7, 11.1 d; $n=35$; individual means]. Individual Estimated Clutch Frequency (ECF) averaged 8.3 ± 0.3 clutches per season [5 to 12 clutches per season; $n=35$ females] and was positively related to the duration of the observed nesting period ($P<0.001$, $R^2=0.91$, $n=35$ females). Over the entire nesting period, the mean clutch size was 86.9 ± 2.2 eggs per clutch [44, 112 eggs, $n=35$ females] for a mean clutch mass of 7.2 ± 0.2 kg [2.6, 10.3 kg; $n=35$ females]. During the entire nesting period, the cumulative clutch size and cumulative clutch mass averaged 717 ± 28 eggs [305, 1129 eggs; $n=35$ females] and 59.7 ± 2.4 kg [30.6, 102.2 kg; $n=35$ females], respectively.

The duration of the observed nesting period and the ECF were positively related to maternal morphometrics (SCCL $P=0.02$, $R^2=0.15$ in both cases; maternal body mass at the first observed clutch $P=0.019$, $R^2=0.15$ and $P=0.01$, $R^2=0.18$, respectively; maternal BCI at first observed clutch $P<0.001$, $R^2=0.31$ and $P<0.001$, $R^2=0.66$, Figure 1, respectively). The cumulative clutch size was positively related to maternal body mass and BCI at the first observed clutch ($P=0.01$, $R^2=0.18$ and $P<0.001$, $R^2=0.34$, respectively) and tended to be positively related to SCCL ($P=0.062$, $R^2=0.10$). The cumulative clutch mass was positively

related to maternal body mass and BCI at the first observed clutch ($P=0.001$, $R^2=0.27$ and $P<0.001$, $R^2=0.41$, Figure 1, respectively) and also to SCCL ($P=0.029$, $R^2=0.13$).

The duration of the observed nesting period was positively related to initial plasma concentrations of urea ($P=0.037$, $R^2=0.12$) and calcium ($P=0.031$, $\rho=0.36$). ECF tended to be positively related to initial plasma concentrations of urea ($P=0.057$, $R^2=0.10$) and was positively related to calcium ($P=0.028$, $\rho=0.37$). The duration of the observed nesting period and the ECF were not related to initial hematocrit or plasma concentrations of TG and glucose ($P>0.13$ in all cases).

Changes in morphometric values throughout the nesting period

A significant but non-linear decrease in maternal body mass was observed throughout the observed nesting period (LME, $P<0.001$, Figure 2a, Table 1). Maternal mass loss was high during the first internesting interval (10 kg) and decreased rapidly during the first 50% of LRE's before stabilising at approximately 5kg between two consecutive clutches thereafter (Wilcoxon tests between successive LRE's classes, $P<0.01$ in all cases, Figure 2b, Table 1). Maternal BCI decreased throughout the nesting period (LME, $P<0.0001$, Figure 2c, Table 1), mostly linearly, although the highest rates were recorded during the first half of the nesting period (Tukey's post-hoc, $P<0.01$ in all cases).

For the 32 females weighed at their last observed clutch, maternal body mass at the last observed clutch was 364.7 ± 7.4 kg [264.6, 440.0 kg], corresponding to mean total body mass loss of 46.8 ± 2.6 kg [23.6, 79.8 kg], i.e., 0.7 ± 0.0 kg.d⁻¹ [0.4, 1.0 kg.d⁻¹]. There was a positive relationship between total maternal body mass loss and maternal body mass at the first observed clutch ($P=0.003$, $R^2=0.54$; $n=32$ females). Maternal BCI at the last observed clutch was -20.6 ± 1.1 [-35.23, 5.8], corresponding to a BCI change of $-188.4\pm 6.6\%$ [-322.3, -132.3] relative to maternal BCI at the first observed clutch. A piecewise regression of maternal BCI

change relative to maternal BCI at the first clutch ($P < 0.001$, $R^2 = 0.77$, Figure 3) revealed a break point at an initial BCI of 18.3, and the BCI loss for the 8 females with an initial BCI < 18.3 was 10-fold higher than for other females (Figure 3). SCCL and SCCW of these 8 individuals did not differ from the other females (t test, $P > 0.2$ in both cases), yet they were lighter at the first clutch (364.1 kg vs 427.3 kg respectively; t test, $P = 0.005$, $t = -3.43$).

Maternal BCI at the last observed clutch was negatively related to the duration of the observed nesting period and to ECF ($P < 0.001$, $R^2 = 0.47$, and $P < 0.01$, $R^2 = 0.58$, respectively). Yet the change of maternal BCI relative to initial BCI was not related to the duration of the observed nesting period or to ECF ($P > 0.28$ in both cases).

Changes in blood values throughout the nesting period

Similarly to morphometric values, hematocrit, glucose, urea and calcium values decreased throughout the nesting period (GEE, $P < 0.0001$, $\chi^2_{wald} = 67.7$; GEE, $P < 0.0001$, $\chi^2_{wald} = 97.2$; GEE, $P < 0.0001$, $\chi^2_{wald} = 35.4$ and GEE, $P < 0.0001$, $\chi^2_{wald} = 60.2$, respectively), and particularly during the first 30% LRE (Wilcoxon paired tests, $P < 0.03$ in each case; Figure 2d, f-h). Thereafter, these parameters did not vary significantly until 70% LRE (Wilcoxon paired tests: $P > 0.06$ in each case), and a slight but significant increase in plasma glucose, urea, and calcium occurred at the very end of the nesting season (Wilcoxon paired tests, $P < 0.03$ in each case; Figure 2d, f-h). Plasma TG decreased throughout the nesting period (LME, $P < 0.0001$, see Figure 2e, Table 1). The decrease was not significant during the first 30% LRE (Tukey post-hoc test: $P > 0.037$) then became significant until the end of the nesting period (Tukey post-hoc tests: $P < 0.001$ in all cases).

Changes in plasma glucose, urea and calcium (measured at the last clutch relative to the first clutch) were not related to the duration of the observed nesting period or to ECF ($P > 0.07$ in all cases). Interestingly, changes in hematocrit and TG levels were positively related to the

duration of the observed nesting period and to ECF (hematocrit: $P < 0.001$, $R^2 = 0.30$ and $P < 0.001$, $R^2 = 0.31$ respectively; TG: $P = 0.033$, $R^2 = 0.11$ and $P = 0.06$, $R^2 = 0.10$ respectively).

Changes in reproductive output throughout the nesting period

Clutch size and clutch mass did not vary throughout the nesting period (LME, $P > 0.14$, LME, $P = 0.059$, respectively, Table 2). Likewise, no changes were observed in mean egg mass over the nesting period (LME, $P = 0.42$).

Discussion

This study aimed to determine whether leatherbacks nesting in French Guiana are capital breeders by assessing whether they experience anorexia during reproduction. We monitored individual body morphometrics and plasma concentrations of metabolites, calcium and hematocrit in 35 gravid females throughout their nesting season.

Morphological evidence of fasting in nesting leatherback turtles

At the onset of their nesting season, leatherbacks nesting in French Guiana weighed on average 410 kg, with a high inter-individual variability since the heaviest individuals (510 kg) were almost twice as heavy as the smallest ones (290 kg). Our results confirm that leatherbacks in French Guiana are heavier and larger than those in other nesting populations (see Georges and Fossette 2006).

In this study, the duration of the nesting period averaged 71 days during which leatherbacks nested every 10 days, laying a total of 8 clutches of 87 eggs each (i.e., 60 kg of eggs in total). These phenology values are consistent with those previously reported in French Guiana (e.g., Girondot and Fretey 1996) and illustrate the extent of reproductive output in this species.

Our longitudinal monitoring shows that the reproductive output was related to maternal morphometrics, with longer, heavier and in better condition females reproducing over a

longer nesting season, laying more clutches, and producing more eggs. In Pacific Costa Rica, larger leatherbacks have been reported to produce larger clutches (Price et al. 2004), despite contradicting results on this population (see Reina et al. 2002; Wallace et al. 2007). Similar positive relationships between maternal size and clutch size have also been reported not only in green and loggerhead turtles (Broderick et al. 2003) but also in other reptiles (reviewed in Shine 2005). In reptiles, such relationships are associated with physical constraints of body size, but also energy stores (Olsson & Shine 1997). The fact that leatherbacks in French Guiana produce larger and more numerous clutches than in other populations (e.g., Pacific Costa Rica; Reina et al. 2002; Price et al. 2004; Wallace et al. 2007; Equatorial Guinea; Honarvar et al. 2011) is thus likely to be related to their larger body size, and may also be related to their better body condition.

During their 71-day nesting period, leatherbacks lost on average 47 kg of body mass, corresponding to about 11% of their body mass at the first clutch. This rate of mass loss (i.e., $0.7 \text{ kg}\cdot\text{d}^{-1}$) is higher than in the green turtle (0.22 ± 0.15 (SD, $n=14$) $\text{kg}\cdot\text{d}^{-1}$ for 166 kg females, i.e., 5% of initial body mass; calculated from Hays et al. 2002) and the hawksbill turtle (0.112 ± 0.1 (SD, $n=75$) $\text{kg}\cdot\text{d}^{-1}$, for 80 kg females, i.e., 7%, Santos et al., 2010) and may result from size-specific differences. The rate of maternal body mass loss decreased non-linearly throughout the nesting season, lowering by about 50% during the first 2-4 weeks before remaining relatively low and stable throughout the rest of the season. This decrease in maternal body mass suggests that leatherbacks nesting in French Guiana do not feed during the internesting intervals, or that feeding may not be efficient enough to maintain body mass throughout reproduction. To date, such patterns in body mass change have not been reported in any other sea turtles, probably because previous longitudinal monitoring were not sufficiently extensive (see Eckert et al. 1989; Hays et al. 2002). Interestingly, clutch mass did not change as the season proceeds, as reported in Pacific leatherbacks (Wallace et al. 2007).

This contrasts however with leatherbacks in Equatorial Guinea where clutch mass decreased through time (Honarvar et al. 2011). Considering maternal body mass loss results from maternal maintenance and egg production, our results suggest that leatherbacks decrease their maintenance throughout the nesting season. Further studies are required to estimate how much maternal maintenance and egg production contribute to maternal mass loss, and to assess physiological and/or behavioural cues involved in the observed patterns.

The body mass lost by leatherbacks was lower than clutch mass, not only when considering any given clutch but also when considering cumulative values over the entire season. The observed discrepancy in mass budget may result from water ingestion during the interesting intervals to supplement maternal body water for egg development. However routes for water loss toward reproduction have not been addressed in the leatherback. Water ingestion may occur by drinking but also by feeding water-rich jellyfish as suggested by Southwood et al. (2005). Interestingly, our results show that hematocrit decreased throughout the season. Decreasing hematocrit is commonly associated with anaemia, i.e. a depressing health status (e.g., Tavares-Dias et al. 2009) and consistent with the decrease in maternal body condition observed throughout the study season. The observation of depressing body condition as the season proceeds suggests that feeding does not occur and that water ingestion is most likely to happen by drinking. Consistently, drinking behaviour has been previously suggested in leatherbacks nesting in French Guiana (Fossette et al. 2008a). We further tested whether jellyfish are actually ingested by assessing plasma metabolite levels throughout the nesting season *via* a complementary longitudinal monitoring of physiological parameters.

Plasma-based evidence of fasting in nesting leatherback turtles

Concurrently with the decrease in morphometric values, significant decreases in plasma concentrations of glucose, TG and urea over the nesting period corresponded to three phases.

During the first 30% of the nesting season, plasma glucose and urea decreased concurrently with steady high levels of TG. During most of the remaining nesting season, plasma glucose and urea then remained low and steady whereas TG decreased linearly through time until the very end of the season, when glucose and urea increased slightly yet significantly. Those profiles of plasma metabolites are similar to those reported in long-term fasting animals (Groscolas et al. 1986; Cherel et al. 1988; Castellini and Rea 1992) and thus strongly suggest that leatherbacks are anorexic during the nesting season (Miller 1997).

At the onset of the season, leatherbacks nesting in French Guiana showed high levels of glucose compared to other leatherback nesting populations (Deem et al. 2006, Harms et al. 2007, Harris et al. 2011, Honarvar et al. 2011), suggesting possible feeding shortly before the first nesting event. After the first clutch, glucose decreased by 30% as also reported in fasting green (32%) and Kemp's ridley (*Lepidochelys kempii*, 36%) turtles (Moon et al. 1999). As the season proceeds, plasma TG decreased dramatically by 50% from the first to the last clutch, as also reported in nesting green turtles (Hamann et al. 2002). In long-term fasting animals, such TG decline has been associated with the mobilization of fat stores (referred as phase II of fasting, Cherel et al. 1988). Besides, the decrease in plasma TG over the nesting period was positively related to the duration of the nesting season and ECF, suggesting that leatherbacks rely chiefly on lipid reserves during reproduction. In sea turtles, body lipids may be stored in large quantities in visceral fat (Moon et al. 1999), the maternal yolk of atretic large follicles (Kuchling and Bradshaw 1993) and in sub-carapace fat (Kwan 1994) particularly in the leatherback (Davenport et al. 2011). Concurrently, the low and steady levels of plasma urea observed from the first third of the nesting season indicate that leatherbacks use a similar protein-sparing strategy to that observed in long fasting birds and mammals (e.g., Cherel et al. 1988). This supports our conclusions that leatherbacks are anorexic during the nesting season in French Guiana, contradicting recent conclusions (Fossette et al. 2008a). A similar

conclusion has been recently proposed in the hawksbill turtle by Goldberg et al. (2012), who reported high levels of leptin, the appetite-suppressing hormone, during the nesting season.

At the very end of the nesting period, urea increased slightly yet significantly. This may indicate a shift from lipid to protein catabolism, as reported during the transition toward the end of long-term fasting whilst lipid body stores are depleted and body proteins are mobilized (phase III, Cherel et al. 1988) and as suggested in green turtles (Hamann et al. 2002). Hormonal refeeding signals (*via* corticosterone) that lead animals to stop reproduction have been reported in sea birds (Groscolas et al. 2008; Spée et al. 2010). Similar hormonal signals may occur in sea turtles and are likely to be mediated by the hunger-stimulating ghrelin, as recently reported in nesting hawksbill turtles (Goldberg et al. 2012). Such hormonal pathways triggering the end of the reproduction should be investigated in leatherbacks.

Evidence of morphological and physiological threshold in nesting leatherback turtles

When considering a maternal Body Condition Index (BCI) based on morphological metrics (SCCL, SCCW and body mass), we showed that all leatherbacks began their reproduction with a positive BCI. Such BCI values has been formerly reported as indicative of the health of individual animals (Peig and Green 2009) and suggests that all leatherbacks had significant amounts of body reserves when entering in reproduction. Considering their reproductive strategy, we expect females should have reached a minimum level of body condition necessary to induce reproduction, as previously reported in capital breeding snakes (Naulleau and Bonnet 1996) and suggested in sea turtles (Hays 2000). Interestingly, the body condition of females starting reproduction with $BCI < 18$ deteriorated dramatically during reproduction compared to others (Figure 3). Furthermore, we showed that females in better condition do indeed lay more clutches during the season than other individuals. This indicates that the costs of reproduction have more deleterious effects on females with poorer body condition.

Consistently, only a small proportion of study females (8 of 32 individuals, i.e., 25%) started reproduction with BCI values below this threshold. The wide range of levels of physiological parameters recorded at the first clutch makes it impossible to identify any particular threshold value for these parameters at the start of reproduction.

At the end of the nesting season, the inter-individual variability in plasma concentrations was very low (Figure 2, Table 1). This may characterise some minimum thresholds associated with the end of reproduction. For instance, BCI values became negative during the period where leatherbacks rely on lipid reserves, suggesting a possible threshold in BCI changes that is associated to the shift in metabolic paths. As far as metabolites are concerned, the shift from lipid to protein metabolism indicates that lipid stores may be a limiting factor for reproduction in leatherbacks. Similarly, the positive relationship we found between plasma calcium and both maternal condition and reproductive output suggests that calcium is a critical component of reproduction in leatherbacks. This may be related to the fact that leatherback's eggs are heavily calcified (about 1.23 g calcium per egg, Bilinsky et al. 2001) and that their large cumulative clutch size may result in high calcium requirements throughout the entire season. The relevance of calcium in leatherback reproduction is further consistent with a recent study showing that hatching and emergence success are related to maternal calcium levels in this species (Perrault et al. 2012).

Drent and Daan (1980) emphasized the importance of body condition in reproduction and postulated that the amount of reserves at the onset of breeding (i.e., the “capital”) acts on the amount of energy devoted to breeding. This is particularly true for capital breeders (Nauelleau & Bonnet 1996). As a whole, our results lead to the conclusion that leatherbacks nesting in French Guiana operate as capital breeders and rely on stored body reserves to ensure their reproduction without jeopardizing their own body condition whilst not feeding during

reproduction. Similar combined approaches should be implemented on other sites where sea turtles have been suggested to feed during the nesting season in order to provide a better understanding of reproductive strategies in these species.

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Table 1. Morphometric and physiological values of the 35 leatherback females monitored throughout the nesting period.

MORPHOMETRICS																	
Body mass (kg)	LRE	Mean	SE	Range	n	Body mass loss (kg)	LRE	Mean	SE	Range	n	Body Condition Index	LRE	Mean	SE	Range	n
	0-10%	443.8	16.2	382.6, 496.6	8		0-10%	-10.1	1.2	-15.4, -5.4	0		0-10%	32.0	3.2	18.9, 45.3	8
	11-20%	404.4	8.5	289.6, 508.0	34		11-20%	-8.3	0.8	-11.6, -3.4	7		11-20%	22.7	1.6	4.7, 44.7	34
	21-30%	408.5	16.4	286.2, 481.4	12		31-40%	-8.3	0.9	-11.6, -5.0	11		21-30%	15.1	2.0	5.7, 28.0	12
	31-40%	385.7	11.6	337.2, 467.2	13		41-50%	-5.6	0.9	-9.6, -3.8	6		31-40%	6.5	1.2	0.1, 15.9	13
	41-50%	381.3	13.2	281.0, 464.0	16		51-60%	-5.1	1.4	-11.2, -2.0	6		41-50%	0.7	0.9	-6.9, 8.2	16
	51-60%	390.6	10.6	339.4, 447.0	12		61-70%	-6.8	1.2	-11.6, -2.0	8		51-60%	-4.8	1.2	-13.1, 0.0	12
	61-70%	396.9	8.8	340.0, 463.2	18		71-80%	-2.9	0.7	-5.6, -1.0	10		61-70%	-6.2	1.0	-13.5, 0.1	18
	71-80%	368.0	10.8	272.0, 429.6	15		81-90%	-5.2	0.8	-8.0, -2.8	6		71-80%	-9.6	1.0	-15.1, -3.6	15
	81-90%	374.8	11.3	299.0, 450.8	18		91-100%	-4.8	0.8	-10.8, -0.6	15		81-90%	-16.7	1.3	-29.1, -8.5	18
	91-100%	364.7	7.4	264.6, 440.0	32								91-100%	-20.6	1.1	-35.3, -5.8	32
PLASMA VALUES																	
Glucose (mmol.L ⁻¹)	LRE	Mean	SE	Range	n	Triacylglycerides (mmol.L ⁻¹)	LRE	Mean	SE	Range	n	Urea (mmol.L ⁻¹)	LRE	Mean	SE	Range	n
	0-10%	13.12	1.22	9.68, 16.88	8		0-10%	14.02	0.90	10.97, 18.03	8		0-10%	1.26	0.18	0.44, 2.12	8
	11-20%	11.95	0.63	8.66, 24.05	33		11-20%	12.59	0.56	5.06, 19.59	33		11-20%	1.04	0.08	0.33, 2.13	33
	21-30%	11.03	0.60	9.06, 17.27	14		21-30%	12.18	0.61	8.15, 16.15	14		21-30%	0.90	0.11	0.53, 2.02	14
	31-40%	9.50	0.33	7.16, 11.15	12		31-40%	9.54	0.77	3.04, 13.26	12		31-40%	0.76	0.04	0.60, 1.13	12
	41-50%	9.06	0.30	7.27, 10.96	15		41-50%	10.43	0.65	7.21, 15.36	15		41-50%	0.78	0.03	0.56, 0.97	15
	51-60%	9.06	0.42	7.62, 12.40	11		51-60%	10.29	0.82	7.46, 16.74	11		51-60%	0.76	0.04	0.57, 0.97	11
	61-70%	8.62	0.25	6.38, 10.66	17		61-70%	8.77	0.68	4.70, 14.99	17		61-70%	0.73	0.02	0.60, 1.02	17
	71-80%	8.11	0.20	7.23, 10.46	15		71-80%	8.06	0.62	4.75, 11.41	15		71-80%	0.69	0.03	0.44, 0.93	15
	81-90%	7.89	0.19	6.81, 9.72	18		81-90%	6.53	0.53	3.42, 11.90	18		81-90%	0.70	0.02	0.63, 0.98	18
	91-100%	8.40	0.17	6.41, 10.70	34		91-100%	5.36	0.43	1.56, 11.89	34		91-100%	0.75	0.03	0.53, 1.25	34
Hematocrit (%)	LRE	Mean	SE	Range	n	Calcium (mmol.L ⁻¹)	LRE	Mean	SE	Range	n						
	0-10%	43.9	1.7	35.0, 50.6	8		0-10%	3.60	0.30	2.71, 5.15	8						
	11-20%	39.7	1.0	26.1, 57.0	33		11-20%	3.14	0.18	1.40, 5.81	33						
	21-30%	38.5	1.2	30.5, 48.4	14		21-30%	2.88	0.15	2.38, 4.46	14						
	31-40%	39.1	2.0	29.0, 53.5	12		31-40%	2.43	0.15	1.22, 3.10	12						
	41-50%	36.2	0.8	31.5, 42.0	15		41-50%	2.83	0.13	2.25, 3.79	15						
	51-60%	35.8	1.0	30.0, 44.0	11		51-60%	2.70	0.20	1.61, 4.18	11						
	61-70%	34.4	1.3	30.0, 52.0	17		61-70%	2.40	0.11	1.49, 3.52	17						
	71-80%	33.9	0.7	30.0, 38.0	15		71-80%	2.50	0.15	1.98, 4.26	15						
	81-90%	35.1	1.3	28.0, 49.5	18		81-90%	2.24	0.09	1.50, 3.36	18						
	91-100%	33.1	0.8	26.0, 48.5	33		91-100%	2.29	0.08	1.39, 3.35	34						

The time scale considered in this study is the Level of Reproductive Effort (LRE; see Materials and Methods section).

Table 2. Reproductive output of the 35 leatherback females monitored throughout the nesting period.

REPRODUCTIVE OUTPUT												
Clutch size (nb of eggs/clutch)	LRE		Mean	SE	Range	n	Clutch mass (kg)	LRE	Mean	SE	Range	n
	0-10%	11-20%										
	0-10%		87.5	10.3	33.0, 130.0	8		0-10%	6.6	0.7	2.6, 8.6	8
	11-20%		87.9	3.9	37.0, 131.0	32		11-20%	7.0	0.3	2.7, 10.3	32
	21-30%		89.8	5.0	59.0, 117.0	13		21-30%	7.7	0.4	5.3, 9.8	13
	31-40%		88.6	3.7	67.0, 113.0	12		31-40%	7.6	0.3	5.7, 9.2	12
	41-50%		92.0	3.9	61.0, 114.0	16		41-50%	7.6	0.4	4.7, 10.1	15
	51-60%		91.5	4.2	59.0, 115.0	13		51-60%	7.7	0.4	5.4, 9.9	10
	61-70%		91.8	2.6	77.0, 112.0	16		61-70%	7.8	0.3	6.5, 9.3	12

The time scale considered in this study is the Level of Reproductive Effort (LRE; see Materials and Methods section).

Figure legends

Figure 1. Relationships between maternal body condition index at first observed clutch and reproductive output indices: number of clutches laid per season (black points, solid line) and cumulative mass clutches per season (white points, dotted line).

Figure 2. Changes in maternal morphometric (a,b,c) and physiological (d, e, f, g, h) values throughout the nesting period (represented by the Level of Reproductive Effort, LRE). Values are means \pm SE. Letters refer to significant differences ($P < 0.05$), numbers refer to the number of individuals represented in each LRE class and vertical dashed grey lines refer to 30% and 70% LRE, where major physiological patterns occurred (see Results section).

Figure 3. Change in maternal body condition index (BCI) over the nesting season. The piecewise regression (solid line) of maternal BCI change (BCI at the last observed clutch relative to BCI at the first observed clutch) (Piecewise regression, $P < 0.001$, $R^2 = 0.77$) revealed a break point, with a dramatic loss of BCI at the offset of the nesting season for females with an initial BCI < 18.3 (white dots, regression slope -15.2) compared to other females (black dots, regression slope -1.3).

Figure 1

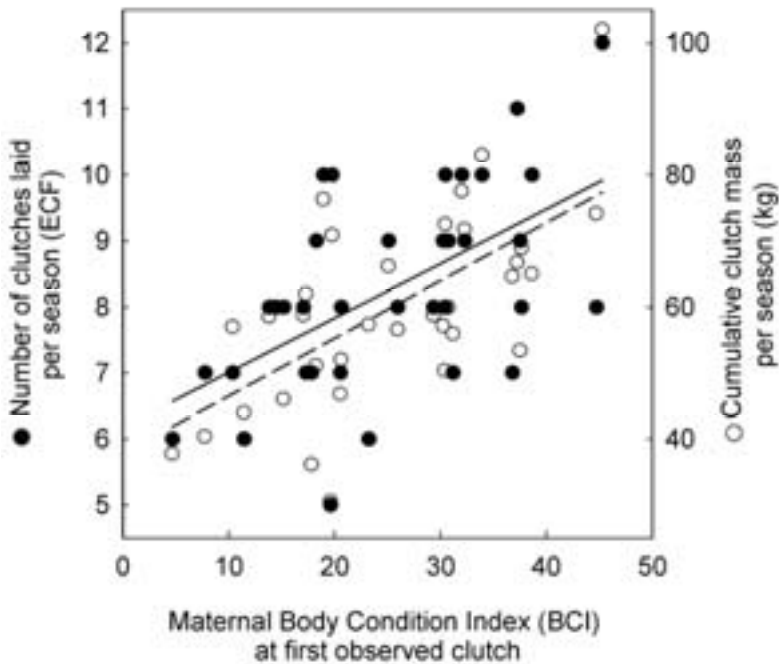


Figure 2

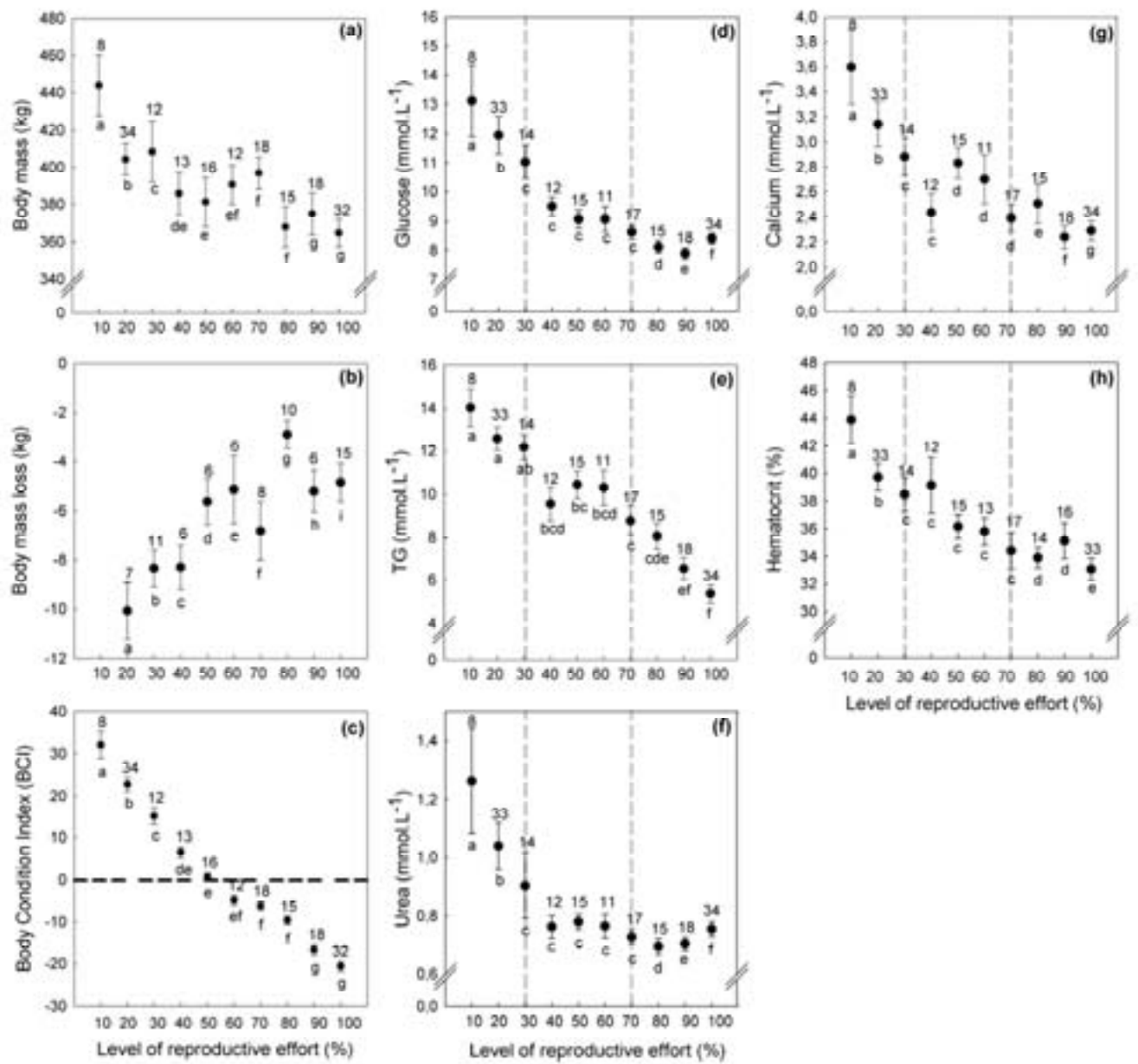
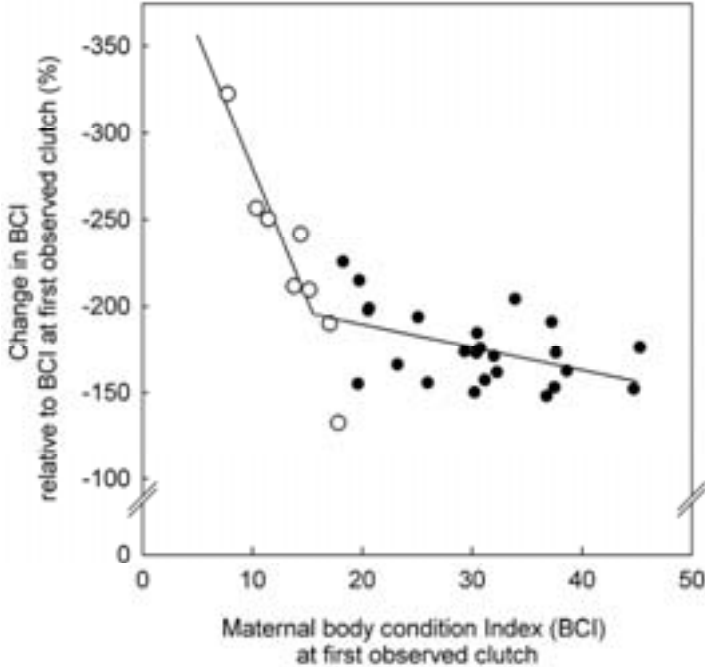


Figure 3



Plastic debris in a nesting leatherback turtle in French Guiana

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Plastic Debris in a Nesting Leatherback Turtle in French Guiana

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ABSTRACT. – We report a field observation of an adult female leatherback turtle (*Dermochelys coriacea*) expelling 2.6 kg of plastic debris from her cloaca while nesting in French Guiana. This field report sustains concerns about plastic ingestion by this endangered species and, further, the impacts of plastic debris to marine wildlife, and points out the needs for effective waste management in both terrestrial and marine habitats.

Plastic pollution is a major threat for marine environments and biodiversity already at risk due to climate change, habitat loss, resource overexploitation, and other anthropogenic disturbances (Derraik 2002). Despite their relatively short history of use on a global scale, plastics represent the main constituent of marine debris worldwide (Ivar do Sul and Costa 2007; Hofer 2008) and will likely remain so for decades to come due

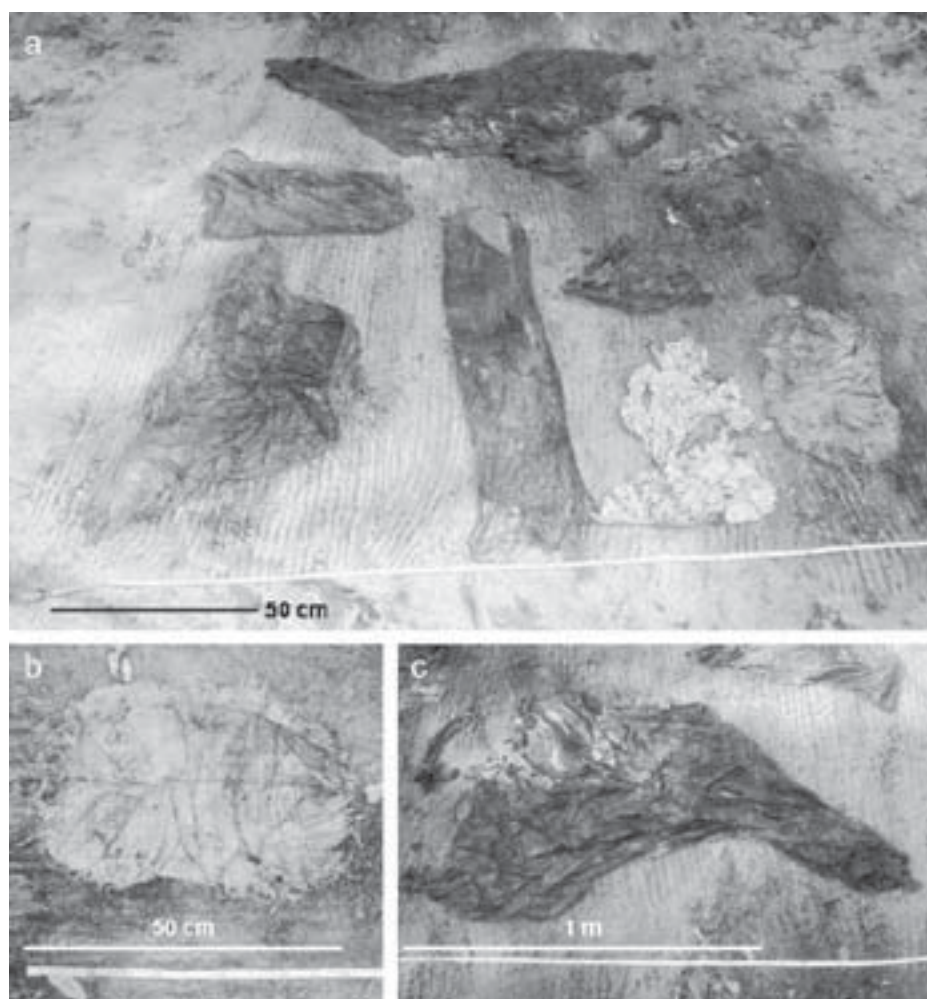


Figure 1. View of the total plastic items (a), including plastic meshed rice bags (b) and plastic domestic rubbish bags (c) extracted from a leatherback turtle attempting to nest in French Guiana (Photo by J.-Y. Georges).

to their slow degradation (Derraik 2002; Hofer 2008). For example, in marine habitats of the wider Caribbean region and Atlantic coast of South America, plastics represent 55% to 70% of marine debris (Ivar do Sul and Costa 2007). Plastic debris affects marine organisms ranging from plankton to large vertebrates (Derraik 2002; Hofer 2008), the latter via entanglement and ingestion (Wallace 1985; Laist 1997; Bugoni et al. 2001; Derraik 2002). Ingestion of plastic debris may occur either because of “mistaken identity” as natural prey by predators or due to incidental ingestion during feeding (Hofer 2008). Debris ingestion has been reported to reduce stomach capacity, feeding stimulus, and growth (Azzarello and Van-Vleet 1987). Plastic ingestion has also been reported to cause internal injuries and intestinal occlusion with potential lethal consequences (Derraik 2002). Partial digestion of plastic items may also result in chemical contamination with detrimental consequences on health, even at low concentrations (Derraik 2002; Hofer 2008).

Among marine megafauna, the leatherback turtle (*Dermochelys coriacea*) is commonly known to face major threats from plastic pollution because individuals of this species are prone to misidentify clear plastic items as jellyfish, their natural prey (Mrosovsky 1981). Here we report a field observation of an adult female leatherback turtle from which a large quantity of plastic debris was extracted from the cloacae during a nesting attempt.

This event occurred during the 2009 nesting season at Awala Yalimapo beach (5°42'N, 53°54'W), French Guiana, a major nesting area for critically endangered leatherback turtles (Fossette et al. 2008b). From March to August, nocturnal patrols were conducted daily to monitor leatherback nesting activity and identify individual turtles (through use of uniquely coded ID tags; Fossette et al. 2008b). On 6 May 2009, we observed a leatherback turtle in apparent distress during nesting: after she excavated her nest chamber, the turtle appeared to be preparing to lay eggs, although instead of eggs, this individual exuded

a greenish liquid with strong odor from the cloaca. Closer inspection revealed that plastic debris was obstructing the cloacal opening. At that point a decision was made to attempt to remove this plastic material. To do so, we gently but firmly pulled by hand these plastic items out of the cloaca. Our efforts yielded a notable quantity of plastic bags and plastic fragments, including those from domestic rubbish bags commonly used in the area as well as woven nylon rice bags (Fig. 1). Once the last of the recoverable plastic material was extracted from the cloaca, the turtle started to deposit white, apparently fresh eggs, as well as rotten eggs. With these 2 egg types also came an abundance of white-colored liquid, and some fresh blood, perhaps indicating that the distal tractus was injured either due to pressure exerted internally by the plastic items or by our manual intervention

Upon recovery, the plastic material was transported to our field station, where it was weighed (± 0.1 kg) using an electronic spring scale and gingerly spread out on sand to determine overall size. In total, 2.6 kg of uncleaned plastic were recovered, including 14 pieces of plastic bag fragments ranging from a few centimeters up to 1.5 m in maximum diameter.

Examination of nesting records for this turtle revealed that it was initially tagged in French Guiana in 2001. This individual was also observed nesting at this beach in 2005 and in 2009 (this study). In 2009, the turtle was observed nesting normally on 15 April and 26 April (V. Plot and J.-Y. Georges, *pers. obs.*, 2009); it was observed again on 6 May when this incident occurred. The turtle was not sighted again after the last event.

Ingestion of plastic debris is a major threat to sea turtles, and leatherback turtles in particular (Mrosovsky 1981), because this species has been known to mistake floating plastic bags for their main prey, jellyfish (Mrosovsky 1981; Mrosovsky et al. 2009). Reports of the occurrence of plastic debris in leatherbacks have increased since the 1960s in the North Atlantic Ocean (Mrosovsky et al. 2009) where leatherbacks feed during their long distance migrations (Ferraroli et al. 2004; Fossette et al. 2010). Because previous reports of plastic ingestion by leatherbacks only concern dead turtles, it has been suggested, perhaps wrongly, that plastic ingestion leads to mortality. Our finding suggests that the ingestion of significant quantities of plastic debris may not be lethal for leatherbacks, and probably for sea turtles in general, as long as it can be expelled. However, because the turtle was not observed afterward, we cannot discuss the actual effects plastic ingestion and manual extraction had on the individual's health and future reproduction.

In sea turtles, intestinal transit time (time between ingestion and first defecation) of soft plastic items has been experimentally estimated to be 9 days in a captive loggerhead turtle *Caretta caretta* (Valente et al. 2008). If this holds for wild leatherbacks, this suggests that the 2.6 kg of plastic bags expelled from the study animal were ingested a few days before our observation. In

French Guiana, gravid leatherbacks spend about 10 days at sea between 2 consecutive nesting events. Then, they remain in French Guiana and Suriname waters, close (< 100 km) to the nesting beach, where they swim continuously over 600 km while performing continuous dives (Fossette et al. 2007; Georges et al. 2007). This suggests that plastic ingestion occurred in regional waters, as supported by the fact that the observed turtle laid several times normally before she expelled plastic debris. This observation additionally supports a recent hypothesis that in French Guiana, gravid leatherback turtles may feed during the nesting season (Fossette et al. 2008a, 2009).

As far as plastic debris is concerned, sea turtles feeding in coastal waters, either during migration (Mrosovsky et al. 2009) or during the nesting season (this study), are of major concern because plastic debris is abundant in these coastal areas due to intensive human activities (e.g., land-based run-off, ship-loading activities; Moore et al. 2001). Their presence in local marine habitats is further concentrated due to local surface currents and bathymetry (Moore et al. 2001; Lattin et al. 2004). The observation described in this account underscores the need for mitigation of plastic pollution in marine ecosystems and points to the need for better environmental management and sustainability.

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Telomeres, age and reproduction in a long-lived reptile

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Telomeres, Age and Reproduction in a Long-Lived Reptile

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Abstract

A major interest has recently emerged in understanding how telomere shortening, mechanism triggering cell senescence, is linked to organism ageing and life history traits in wild species. However, the links between telomere length and key history traits such as reproductive performances have received little attention and remain unclear to date. The leatherback turtle *Dermochelys coriacea* is a long-lived species showing rapid growth at early stages of life, one of the highest reproductive outputs observed in vertebrates and a dichotomised reproductive pattern related to migrations lasting 2 or 3 years, supposedly associated with different environmental conditions. Here we tested the prediction of blood telomere shortening with age in this species and investigated the relationship between blood telomere length and reproductive performances in leatherback turtles nesting in French Guiana. We found that blood telomere length did not differ between hatchlings and adults. The absence of blood telomere shortening with age may be related to an early high telomerase activity. This telomere-restoring enzyme was formerly suggested to be involved in preventing early telomere attrition in early fast-growing and long-lived species, including squamate reptiles. We found that within one nesting cycle, adult females having performed shorter migrations prior to the considered nesting season had shorter blood telomeres and lower reproductive output. We propose that shorter blood telomeres may result from higher oxidative stress in individuals breeding more frequently (i.e., higher costs of reproduction) and/or restoring more quickly their body reserves in cooler feeding areas during preceding migration (i.e., higher foraging costs). This first study on telomeres in the giant leatherback turtle suggests that blood telomere length predicts not only survival chances, but also reproductive performances. Telomeres may therefore be a promising new tool to evaluate individual reproductive quality which could be useful in such species of conservation concern.

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Introduction

One of the principal aims of evolutionary ecology is to understand what causes variations in individual fitness. Individuals performing better in terms of survival and reproduction are commonly qualified as “good quality” individuals. This concept is widely used in evolutionary ecology but has rarely been defined in detail and remains difficult to measure [1]. A first step may consist of determining whether individual quality is genetically mediated through natural selection [1], a hypothesis that can be tested using telomere length measurements. Telomeres are repetitive non-coding DNA sequences that cap the ends of eukaryote chromosomes and shorten through successive DNA duplications (i.e. at each cell's division) until they reach a critical length causing chromosome instability, cell senescence and ultimately cell death [2]. Although telomere length is not necessarily a reliable marker of age, the individual variability in telomere length and telomere shortening has been positively related to longevity or survival across species [3] but also within them [4]. Individual variability of telomere length at a given age is currently explained by the acceleration of telomere loss by stressors (e.g. oxidative stress [5]) which may have significant impact during early growth (e.g. during

accelerated growth [6–8]). Telomere loss may however be reduced by telomere maintenance mechanisms such as telomerase activity [9]. Interestingly, although telomere loss with age seems to be the general rule in animals [10], some species are characterized by an unexpected positive relationship between telomere length and age including species such as the Leach's storm petrel [3], the sand lizard (*Lacerta agilis* [11]) and the water python (*Liasis fuscus* [12]). This leads us to question whether telomere length shortening with age really is a general pattern in the animal kingdom.

The recent use of telomere length as an ageing proxy by ecologists has led to interesting hypotheses concerning sex-specific inheritance and telomere length dynamics in relation to sex-specific life-history strategies [13,14]. While females have been reported to have longer telomeres than males ([15,16] but see [17] for a critical review) it has been suggested that telomeres are better predictors of lifetime reproductive success in females than in males, thus favouring selection of longer telomeres in females [14]. Yet the important question of whether telomere dynamics provide any useful information regarding organisms' fitness related-traits (e.g. reproductive success) still needs to be investigated further in different species before being generalized [18].

In light of this context, we investigated telomere length in the leatherback turtle *Derموchelys coriacea*. The leatherback turtle displays many unusual life history traits such as rapid early (and thereafter continuous) growth [19], gigantothermy [20] and high reproductive potential [21] interspersed with pluri-annual interbreeding oceanic migrations. This makes it an ideal model for (1) testing the prediction of telomere shortening with age *via* the comparison of telomere length in leatherback hatchlings and adult females and (2) investigating the potential relationships between telomere length and individual reproductive strategy.

Materials and Methods

Ethics Statement

This project respected the legal requirements of the country in which the work was carried out and followed all institutional guidelines. This study was carried out under CNRS-IPHC institutional license (B67 482 18 delivered by Departmental Direction of the Veterinary Services, Strasbourg, France; and Police Prefecture of Bas-Rhin) and individual licences to JYG (67–220 delivered by the Departmental Direction of the Veterinary Services, Strasbourg, France; and the Police Prefecture of Bas-Rhin; and 973-5/0703039 delivered by the Police Prefecture of French Guiana). Licences covered all field studies and animal experiments, i.e. clinical monitoring of living animals (including biometric measurements and weighing) and sampling on living animals (including blood sampling). Turtles were captured by JYG holder of licenses and VP themselves. All field procedures (except weighing) were performed during oviposition on the natural nesting beach without holding or contention. Biometric measurements and blood sampling were performed once oviposition was initiated for preventing the turtle to abandon its natural nesting behaviour. Biometric and sampling procedures lasted in total 1 minute over the 15 minutes turtles need for laying eggs. Blood samples were collected from the turtles for routine diagnostic purposes (monitoring health, feeding and hormonal states) which include the one specifically concerned by the present study. Weighing occurred after oviposition when the turtle was heading back to the sea. Then, a custom-made harness with four 10 cm wide nylon straps was placed on the sand in front of the turtle, which was secured when the turtle was lying on it. A 4.5 m tall carbon-fibre tripod was immediately placed above the securely harnessed turtle. The turtle was then lifted using a hoist on which an electronic spring scale. Harnessing, lifting, reading the weight, bringing the turtle back down on the sand and releasing the harness lasted in total 5 minutes. Every turtle was individually observed remotely after releasing the harness to ensure she reached safely the sea.

The leatherback turtle is listed as critically endangered at the world scale by the IUCN. The area where the fieldwork was performed is part of the Natural Reserve of Amana.

Field Work

During their reproductive life, sea turtles alternate pluri-annual migrations and reproductive seasons, the latter relying entirely on the use of body reserves stored during the previous migration. During a given reproductive season that may last 2–3 months, females successively lay several clutches during short (2-h) nocturnal landings separated by inter-nesting intervals of ~10 days at sea [22].

The study site was located at Awala-Yalimapo (5.7°N, 53.9° W), French Guiana, South America, where one of the world's largest nesting populations of leatherback turtles is located [23]. The study area consisted in a 4-km long stretch of sandy beach that was

patrolled every night from 6 pm to 7 am throughout the nesting season (March–July) in 2005 and 2006. There gravid females are individually identified thanks to a long-term tagging program and individually monitored through a pluri-annual capture/mark/recapture (CMR) protocol [23]. This permitted to record the identity and the date of oviposition of every turtle encountered during the considered seasons and to assess the year of their preceding nesting season. Based on similar data, leatherback turtles breeding in French Guiana have been reported to nest mainly every 2 or 3 years [24].

This study concerned 42 adult leatherback females that were regularly observed and captured during the nesting events in 2005 or 2006. For every encounter, individuals' biometric measurements (Standard Curvilinear Carapace Length, SCCL; Standard Curve Curvilinear Width, SCCW; and body mass) were performed following Georges and Fossette [25]. During the oviposition period, blood samples (~6 mL) were collected in a heparinised syringe via venipuncture of a venous sinus in the hind flipper. The blood was then transferred to polypropylene microtubes before being placed in a cool box and transported to our field station for centrifugation. Red blood cells and plasma were then separated and placed in Eppendorf tubes and stored at –20°C until laboratory analyses were carried out (see below).

This study focused on adult leatherbacks whose previous reproduction was known thanks to the above-mentioned CMR monitoring already in place on the study site. For these considered individuals, the duration of the migration preceding the nesting season, hereafter referred as RI duration, was estimated by calculating the number of years elapsed between the observed nesting season and the preceding one thanks to the pluri-annual CMR monitoring. This permitted to distinguish individuals with RI of 2 years versus 3 years, as reported by [24], for further comparisons. For example, individuals observed nesting in 2005 were considered as 2-yr and 3-yr remigrants when lastly observed nesting in 2003 and 2002, respectively. The reproductive output during the given nesting season was estimated, and is referred to the Estimated Clutch Frequency (ECF, [26,27]). The ECF is the total number of clutches that a turtle is believed to have deposited during its nesting season and takes the intermediate unobserved clutches into account (based on the mean inter-nesting duration of 10 days in leatherbacks [27–29]) between the first and the last clutch observed.

In addition, in 2009, 20 hatchlings freshly killed by predators were collected, biometric measurements (SCCL, SCCW and body mass) were performed and blood samples were taken. Blood samples were then stored at –20°C until laboratory analyses were carried out.

Laboratory Analyses

Analyses were carried out at the CNRS-IPHC, Strasbourg, France, following the procedure described by Criscuolo *et al.* [30]. DNA was extracted from 5 µL of red blood cells using a commercial kit (DNeasy Blood and Tissue Kit, QIAGEN). We then performed quantitative Polymerase Chain Reaction (qPCR) assay to measure telomere length, using the method described by Criscuolo *et al.* [30] and adapted to sea turtles. This method [31] determines relative telomere length by measuring within each DNA sample the factor by which it differs from a reference DNA sample in its ratio of telomere repeat copy number (T) to a control gene (C) that was predetermined to be non variable in copy number among the studied population (non-VCN, [32]): i.e. the T/C ratio. This method is widely used for intraspecific comparisons [4,33–35] and has been validated by measurements made on the same samples using qPCR method and telomere restriction

Table 1. Models of the effects of blood telomere length and individual body condition index (BCI) on individual annual reproductive output (ECF) in leatherback turtles nesting in French Guiana in 2005 or 2006.

Model 1 : ECF ~ BCI + Telomere length + BCI : Telomere length (with 1st degree integration); df=20; F=3.025; p=0.0565; AIC=97.931				
Model 2 : ECF ~ BCI + Telomere length; df=20; F=4.759; p=0.021; AIC=95.979				
	Estimate	Std. error	t-value	p
Intercept	6.57	0.54	12.185	<0.001
BCI	0.53	0.45	1.185	0.251
Telomere length	0.56	0.20	2.786	0.011
Model 3 : ECF ~ Telomere length; df=20; F=7.952; p=0.011; AIC=95.548				
	Estimate	Std. error	t-value	p
Intercept	6.55	0.54	12.03	<0.001
Telomere length	0.576	0.20	2.82	0.010

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turtles (*Chelonia mydas*, [41]). Therefore, the exact impact of migration duration on reproductive output demands further study.

On the other hand, the dichotomy in migration duration in leatherbacks nesting in French Guiana has been proposed to be related to distinct feeding areas in the Atlantic ocean [42], with individuals feeding in the more southern and coastal areas of West Africa extending their migration by one year compared to individuals feeding in northern oceanic areas [43]. The difference in telomere length reported in the present study may be related to different thermoregulatory constraints during the migration. Indeed higher metabolic costs associated with thermoregulation in northern, cooler, waters during 2-yr migrations may result in higher oxidative stress and ultimately in shorter telomeres. Importantly, individuals may migrate alternatively over 2 or 3

years depending on their nutritional status. Such switching in migration duration may result in complex telomere dynamics throughout an individual lifetime, through varying telomerase activity. Indeed, if telomerase activity reported in somatic tissues of many reptile species [44] holds in sea turtles, delaying intermittently reproduction for one supplementary year may offset previous telomere loss. Long-term longitudinal studies are required to further investigate the potential links between migratory patterns and behaviour, reproductive pattern (breeding every two or three years) and associated reproductive output and hence determine the causes and effects of telomere dynamics on reproductive strategies.

Finally we found no differences in blood telomere length between hatchlings and adults. As the hatchlings considered in our study were individuals predated before reaching the sea, they could be considered poor quality, with shorter telomeres than the hatchlings that do survive. However, the hatchlings used in our study were of a similar weight to successful leatherback hatchlings (44.4 ± 4.16 g, [22]), suggesting this was not the case. Another pitfall when interpreting cross-sectional sampling, which is the case in our study, is that telomere erosion with age may be hidden by the selection of individuals with long telomeres [37]. Yet the longitudinal study of such a relationship in leatherbacks presents technical and logistical constraints: to the best of our knowledge, it is impossible to sample the same individuals from hatchling to adult stages, particularly in the wild. Our results are similar to the unique study published so far on sea turtle telomeres where no correlation was found between blood telomere length and age in captive loggerhead turtles [45]. Yet older individuals tended to have shorter telomeres in epidermis samples [45]. Based on our results and on other studies using telomere length measurements from blood samples, we suggest that the apparent lack of telomere loss with age we found may be attributed to the absence of telomere-based senescence reported in many species of Chelonian [44]. Furthermore, in animal species such as sea turtles where individuals have fast early growth and continuous growth throughout their life, it has been proposed that high telomerase activity (*i.e.* the restoring enzyme of telomeres) occurs in somatic tissues [12]. This process preserves the proliferation capacity of cells during high-rate cell division (generally associated to early growth) through the limitation of telomere loss and can hence prevent senescence [46]. This mechanism has been proposed to be a general characteristic of squamate reptiles [13,44] and may

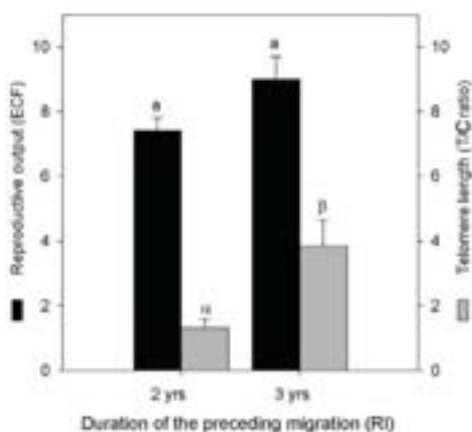


Figure 1. Estimated Clutch Frequency (ECF, the estimated number of clutches laid during the considered nesting season) and blood telomere length in relation to the duration of the migration preceding the considered nesting season (RI, the remigration interval) in leatherback turtles nesting in French Guiana in 2005 or 2006. ECF did not differ according to RI, but tended to be lower for 2-yr RI. Blood telomeres were significantly shorter in females with 2-yr versus 3-yr RI. Letters refer to test significance for ECF and T/C ratio separately. Values are means \pm SE. doi:10.1371/journal.pone.0040855.g001

occur in the leatherback turtle, which is considered to be the fastest-growing turtle [19]. In the sand lizard the fitness of females has been reported to primarily depend on reproductive lifetime and telomere maintenance (*i.e.* telomerase activity) and is therefore subjected to positive selection, unlike males [13]. Such a process, preventing telomeres from early attrition thanks to some telomerase activity, would be beneficial to the survival of leatherback females and may thus represent an adaptive strategy. Assessing telomerase activity in somatic tissues of hatchlings, adult male and female leatherback turtles could be a future step to test this hypothesis. An intriguing issue is also that telomerase activity has been described as inversely related to body mass in rodents, a result interpreted as an anti-tumor protection process [47]. If future studies confirm that telomere length is preserved in adult leatherback turtles (*i.e. a fortiori* through telomerase activity), it would imply a different evolution of the trajectories of control pathways in ageing and cell proliferation by telomeres in testudines.

Monaghan & Haussman [48] stated: “there is a clear need to broaden the range of organisms studied [with respect to telomere dynamics] in order to encompass more variable life histories”.

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7. ANNEXES



**Atlantic leatherback migratory paths
and temporary residence areas**

**S Fossette, C Girard, M Lopez-Mendilaharsu, P Miller, A Domingo, D Evans, L
Kelle, V Plot, L Prosdocimi, B Verhage, P Gaspar & J-Y Georges (2010)**

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Atlantic Leatherback Migratory Paths and Temporary Residence Areas

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Abstract

Background: Sea turtles are long-distance migrants with considerable behavioural plasticity in terms of migratory patterns, habitat use and foraging sites within and among populations. However, for the most widely migrating turtle, the leatherback turtle *Dermodochelys coriacea*, studies combining data from individuals of different populations are uncommon. Such studies are however critical to better understand intra- and inter-population variability and take it into account in the implementation of conservation strategies of this critically endangered species. Here, we investigated the movements and diving behaviour of 16 Atlantic leatherback turtles from three different nesting sites and one foraging site during their post-breeding migration to assess the potential determinants of intra- and inter-population variability in migratory patterns.

Methodology/Principal Findings: Using satellite-derived behavioural and oceanographic data, we show that turtles used Temporary Residence Areas (TRAs) distributed all around the Atlantic Ocean: 9 in the neritic domain and 13 in the oceanic domain. These TRAs did not share a common oceanographic determinant but on the contrary were associated with mesoscale surface oceanographic features of different types (i.e., altimetric features and/or surface chlorophyll *a* concentration). Conversely, turtles exhibited relatively similar horizontal and vertical behaviours when in TRAs (i.e., slow swimming velocity/sinuuous path/shallow dives) suggesting foraging activity in these productive regions. Migratory paths and TRAs distribution showed interesting similarities with the trajectories of passive satellite-tracked drifters, suggesting that the general dispersion pattern of adults from the nesting sites may reflect the extent of passive dispersion initially experienced by hatchlings.

Conclusions/Significance: Intra- and inter-population behavioural variability may therefore be linked with initial hatchling drift scenarios and be highly influenced by environmental conditions. This high degree of behavioural plasticity in Atlantic leatherback turtles makes species-targeted conservation strategies challenging and stresses the need for a larger dataset (>100 individuals) for providing general recommendations in terms of conservation.

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Introduction

Many species show considerable behavioural plasticity in terms of foraging and habitat use in response to fluctuations in environmental conditions and prey availability [1–5], or to changes in energetic requirements associated with the different stages of the annual cycle (e.g., reproduction, migration [6–8]). In addition, a high degree of

phenotypic plasticity usually exists between geographically separate populations experiencing different ecological conditions. For instance, rockhopper penguins *Eudyptes chrysocome* from three different colonies in the Indian Ocean have been reported to show significant differences in diving behaviour and foraging effort with consequences on life history traits such as chick growth [9]. Similarly, gravid green turtles *Chelonia mydas* have been shown to

exhibit contrasted, probably food-mediated, patterns of depth utilisation between Ascension Island (mid-Atlantic) and northern Cyprus (Mediterranean Sea) [10].

High degree of behavioural plasticity within a species may make species-targeted conservation strategies more difficult to implement. For instance, Cape gannets *Morus capensis* from two colonies off South African coasts show contrasted foraging strategies: birds from one colony feed on natural prey, i.e. pelagic fish targeted by fisheries, while occupants of the second colony feed mainly on fishery wastes [11]. Therefore some fisheries may increase food availability for gannets through waste while other fisheries compete directly with the birds when harvesting their main natural prey, making the implementation of any conservation policies in this area particularly challenging [12–14]. This example highlights the difficulty of implementing efficient conservation strategies at a species level without taking into account inter-population variability in terms of foraging and dispersal behaviour.

Sea turtles are long-distance migrants that exhibit a high variability in migration destination among individuals of a same population and among populations [15]. The potential determinants of migration destination have recently been investigated in the loggerhead turtle *Caretta caretta* from a major rookery in the Mediterranean [16]. It appeared that the pattern of adult dispersion from the breeding area closely matched the different drift scenarios that would have been experienced by hatchlings as they first left their natal beach. In their early lives as they passively drift in ocean currents, turtles may explore different habitats and potential future foraging areas. Then, as adults, they may use this initial experience to migrate to predictable foraging sites. This hypothesis of “hatchling drift scenarios” has also been suggested to explain the genetic connectivity between geographically distant populations of green turtles [17].

The critically endangered leatherback turtle, *Derموchelys coriacea*, performs the longest migration of any sea turtle and disperses throughout all the ocean basins (e.g., [18–22]) to forage on patchily-distributed jellyfish [23]. Many studies have investigated in details the diving, foraging and dispersal behaviour of leatherback turtles and show a high degree of variability among individuals of the same population [19–21,24–35]. Yet, to date only one study described the spatio-temporal foraging patterns of satellite-tracked leatherback turtles from different nesting and foraging sites in the North Atlantic [27]: this study showed a similar degree of behavioural variability among individuals and among populations in Atlantic leatherback turtles.

Here, we investigated the movements and diving behaviour of both north and south Atlantic leatherback turtles during the post-breeding migration of 12 individuals from three different nesting sites and 4 individuals captured at one foraging site to assess the potential determinants of intra- and inter-population variability in migratory patterns. We particularly focused on oceanographic conditions encountered by the turtles during the migration in order to test potential hatchling drift scenarios at the Atlantic Ocean scale.

Methods

Ethics statement

This study adhered to the legal requirements of the countries in which the work was carried out, and to all institutional guidelines. Fieldwork in French Guiana and Suriname was carried out under CNRS-IPHC institutional license (B67 482 18) and individual licences to JYG (67-220 and 04-199) and SF (67-256) delivered by the National Committee of Nature Protection (French Ministry of Ecology and Sustainable Management), Paris, France; the

Departmental Direction of the Veterinary Services, Strasbourg, France; and the Police Prefectures of Bas-Rhin and French Guiana. In Uruguay the fieldwork was conducted by Karumbe under a permit of scientific capture and collection (# 73/08) from the Fauna Department - Ministry of Cattle, Agriculture and Fishing. In Gabon, fieldwork was conducted by WWF Gabon which has an “accord de siege” (i.e. “headquarter agreement”) from the Ministère des Eaux et Forêts of Gabon and who has been recognized to do fieldwork on marine turtles in this area since 2002. In Panama, fieldwork was conducted by Caribbean Conservation Corporation under the permits SE/A-55-04 and SE/A-48-05 delivered by the Autoridad Nacional del Ambiente (ANAM).

Turtles and satellite tracking

Sixteen satellite transmitters (Series 9000 Satellite Relayed Data Loggers SRDLs, manufactured by the Sea Mammal Research Unit, St. Andrews, United Kingdom) were deployed on leatherback turtles between June 2005 and October 2006 (**Table 1**) within the Trans-Atlantic Leatherback Conservation Initiative (TALCIN, see acknowledgements). Three tags were deployed on the Caribbean coast of Panama at Chiriqui beach (9.0°N-81.7°W), one in Suriname at Samsambo beach (5.8°N-54.0°W), five in French Guiana at Awala-Yalimapo beach (5.7°N-53.9°W) and three in Gabon at Kinguere beach (0.2°N-9.2°W). One turtle was equipped in Uruguay at Kiyu (34.7°S-56.7°W) after it was incidentally captured by an artisanal bottom-set gillnet, and three were equipped in international waters of the Southwestern Atlantic (29.5°S-41.7°W; 28.3°S-44.0°W and 28.2°S-44.3°W respectively) after they were incidentally captured by Uruguayan pelagic longliners. Among these 16 turtles, 14 were mature females, one was a mature male (UR06-2) and one a subadult (UR06-1; **Table 1**). Most of the tagged animals were females as, for logistical reasons, fieldwork mainly occurred at the nesting sites. Some of these tracks have been previously published [20,26,36] but not the post-breeding migrations of the turtles nesting in Gabon, which are described for the first time in the present study. For all turtles, SRDLs were attached on the pseudocarapace using custom-fitted harness systems except for two turtles (FG05-4 and FG05-5) for which SRDLs were directly attached to the carapace [36].

Turtle movement analysis

Turtle movements were reconstructed using the Argos satellite location system (www.cls.fr). Inter-nesting tracks occurring during the nesting season were not included in the analysis. All tracks were processed in a similar way as in Gaspar et al. [37]: all locations of all accuracies were analysed, however Argos locations implying an apparent speed above $2.8 \text{ m}\cdot\text{s}^{-1}$ (i.e. $>10 \text{ km}\cdot\text{h}^{-1}$) were discarded as travel rates above this threshold are considered as biologically unlikely [32]. Tracks were then smoothed and re-sampled every 3 hours. This sampling interval provides a spatial resolution sufficient for sampling the mesoscale variations of the ocean current fields and thus correctly estimating the currents along the tracks (see below). A local linear regression with a time window of two days was used to re-sample the tracks. Epanechnikov kernel was used to weigh observations in that window, and eventually adjust the size of the window according to the quality of the data in order to avoid over-smoothing the tracks. Re-sampled tracks (hereafter referred as apparent path) were analysed in three ways, as described below.

First, thanks to the regular re-sampling interval used, we calculated the time spent in 1° latitude by 1° longitude areas along the apparent paths in order to distinguish sections where turtles

Table 1. Summary of the movements of 16 Argos tracked leatherback turtles during their migration between 2005 and 2008.

Turtle	Deployment location	SCCL (cm)	Sex	Date of departure	Track duration (days)	Minimum travelled distance (km)
FG05-1	French Guiana	147	F	26 Jul 2005	164	6048
FG05-2	French Guiana	160	F	26 Jul 2005	410	9971
FG05-3	French Guiana	-	F	28 Jul 2005	258	7048
FG05-4	French Guiana	-	F	27 Jul 2005	103	5212
FG05-5	French Guiana	149	F	25 Jul 2005	113	6005
SU05-1	Surinam	148	F	25 Jun 2005	715	14154
PA05-2	Panama	152	F	13 Jun 2005	632	17614
PA05-4	Panama	152	F	08 Jul 2005	362	9200
PA05-5	Panama	156	F	16 Jun 2005	324	11289
GA06-1	Gabon	160	F	04 Mar 2006	533	11096
GA06-2	Gabon	163	F	05 Mar 2006	109	2834
GA06-3	Gabon	143	F	05 Mar 2006	299	6120
UR05-1	International waters	148	F	15 Jun 2005	314	8184
UR06-1	International waters	126	unknown	14 Aug 2006	340	6636
UR06-2	International waters	159	M	31 Jul 2006	237	5957
UR06-3	Uruguay	156	F	29 Oct 2006	631	15362

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spend significantly more or less time, hereafter referred as Temporary Residence Areas (TRAs) and transit areas, respectively. When considering the cumulative frequency distribution of the time spent per $1^\circ \times 1^\circ$ area, the curve reveals an inflection at the y-point corresponding to 90 hours (i.e. 76.1%). Accordingly, we considered that for each turtle, a TRA could be defined as $1^\circ \times 1^\circ$ area where the animal spent at least 90 h. All tracks were thus divided into several sections (TRA vs transit) for which behavioural parameters were calculated (see below).

Secondly, due to the impact that ocean currents may have on an animals' movements [37–39] we estimated the surface currents experienced by each individual in order to distinguish the animal's apparent path (including a current drift component) from its own swimming motion (hereafter referred as motor path). In short, this consisted of computing surface velocity fields on a daily basis, by summing the geostrophic and Ekman components deduced from altimetry and wind stress data, respectively (www.aviso.oceanobs.com). Then, at each 3-h re-sampled location, we calculated (1) an apparent velocity, (2) a local surface current velocity and (3) a swimming velocity, corresponding to the difference between the apparent and the current velocities. This current correction was performed for all turtles except those remaining at low latitudes ($<10^\circ$) where geostrophic approximations break down [37].

Last, we considered that an animal could stay in any given TRA either by decreasing its travel rate or by modifying the spatial structure of its apparent path, i.e. its apparent path straightness. Straightness variations can be detected along a path by successively measuring the ratio D/L for path sections with a constant length L . Consistently, each apparent path was re-sampled in a form of a sequence of n steps with a constant length l ($l = 15$ km in the present study, corresponding to the average distance between our successive Argos locations), and the ratio D_i/L was successively calculated for each location (x_i, y_i) at the centre of a 10-steps ($L = 150$ km) window, i.e. between location (x_{i-5}, y_{i-5}) and location (x_{i+5}, y_{i+5}) . To further investigate the relation between the apparent path and the swimming behaviour of the turtle, the same procedure was applied to the motor paths.

Turtle diving behaviour

SRDLs provided measurements of diving behaviour from a pressure sensor, which sampled depth every 4 seconds with an accuracy of 0.33 m. Data were statistically summarised onboard over 6-h collection periods providing the number of individual shallow (between 2 and 10 m) and deep (>10 m) dives performed during the period, their mean (\pm SD) duration and mean (\pm SD) maximum depth, as well as the proportion of time spent at the surface and diving (in shallow or deep waters). SRDLs continuously logged summaries but only a sample of these data was relayed by satellite because of the limited bandwidth of the Argos link. For each temporary residence/transit area identified as above, the above mentioned dive parameters were averaged for statistical analyses.

Satellite-derived oceanographic data

In addition to the estimation of the surface current fields (see above), the oceanographic regions crossed by the turtles were characterised using bathymetry, chlorophyll a data and altimetry. Bathymetry data were issued from the National Geophysical Data Center, National Oceanic and Atmospheric Administration, U.S. Department of Commerce, at a spatial resolution of $1/30^\circ$ (ETOPO2v2; www.ngdc.noaa.gov). The seafloor regimes were subdivided as follows: neritic (i.e. continental shelf waters (<200 m) and shelf slope (200 to 2000 m)) and oceanic (>2000 m). Chlorophyll a surface concentration was described using monthly grids produced by the SeaWiFS project (spatial resolution of 9 km; <http://web.science.oregonstate.edu/ocean.productivity/>). Altimetry data obtained from AVISO (www.aviso.oceanobs.com) provided weekly maps of sea level anomaly (MSLA) and maps of absolute dynamic topography (MADT) on a $1/3 \times 1/3^\circ$ Mercator grid. Both MSLA and MADT data underwent a time linear interpolation to obtain daily gridded fields.

Drifter data

To assess the potential drift scenarios of passive particles from our different tagging sites, we used the Global Lagrangian Drifter

Data (<http://www.aoml.noaa.gov/envids/>). This dataset consists of satellite-tracked buoys drogued near the surface (15 m) from 1979 to the present. Drifter locations are estimated from 16 to 20 satellite fixes per day, per drifter. The Drifter Data Assembly.

Center (DAC) at NOAA's Atlantic Oceanographic and Meteorological Laboratory (AOML) assembles these raw data, applies quality control procedures and interpolates them via kriging to regular 6-h intervals. Here we selected satellite-tracked buoys that have passed within a window with $\pm 5^\circ$ of amplitude in longitude and latitude (1) centred on each tagging site or (2) centred on a particular TRA.

Results

Migration patterns

Tracking duration of the sixteen turtles ranged from 103 days (FG05-4) to 715 days (SU05-1) for recorded distances ranging from 2834 to 17 614 km (**Table 1**). Distinct dispersal patterns were observed according to the tagging location and 22 Temporary Residence Areas (TRAs) were identified (**Fig. 1**).

Suriname - French Guiana complex. The six females which left French Guiana and Suriname between June and July 2005 dispersed widely but remained into the North Atlantic. Four females dispersed north-eastward (FG05-1, FG05-2, FG05-3 and FG05-4), reaching the Azores Front (between 34°N and 41°N , TRA1) at the end of summer/beginning of autumn. They spent

between several weeks to several months in this oceanic area before three of them headed south at the end of autumn/beginning of winter towards the Cape Verde islands. One female headed north-westward (FG05-5) and reached the Eastern continental shelf of USA (TRA2) in October 2005 where she remained until transmission stopped one month later. The last female (SU05-1) dispersed eastward reaching the Guinea Dome area (between 10°N - 14°N and 23°W - 19°W , TRA3) in October 2005. She stayed in this oceanic area until March 2006 before reaching the Mauritania upwelling area (TRA4) where she remained for two months. In May, she travelled north to the Bay of Biscay (TRA5) where she spent one month. In November, she moved south and spent the next six months until June 2007 off the coasts of Portugal (TRA6).

Panama. Two out of the three turtles equipped in Panama in July 2005 and June 2006 dispersed in the Gulf of Mexico while the third one reached the North Atlantic. After crossing the Caribbean Sea in one month, one turtle (PA05-4) explored the eastern side of the Gulf of Mexico spending two months (Sep-Oct 2005) along the north-eastern continental slope (TRA7) and four months (Nov 2005-Mar 2006) south of the Loop Current (TRA8). The second turtle (PA05-5) first moved towards the Northern continental shelf of the Gulf of Mexico (TRA9) and then travelled to the Western and South-western shelves of the Gulf (TRA10) from August to September 2006 towards an area between Vera Cruz and Yucatan (Mexico) where she remained during six months until March

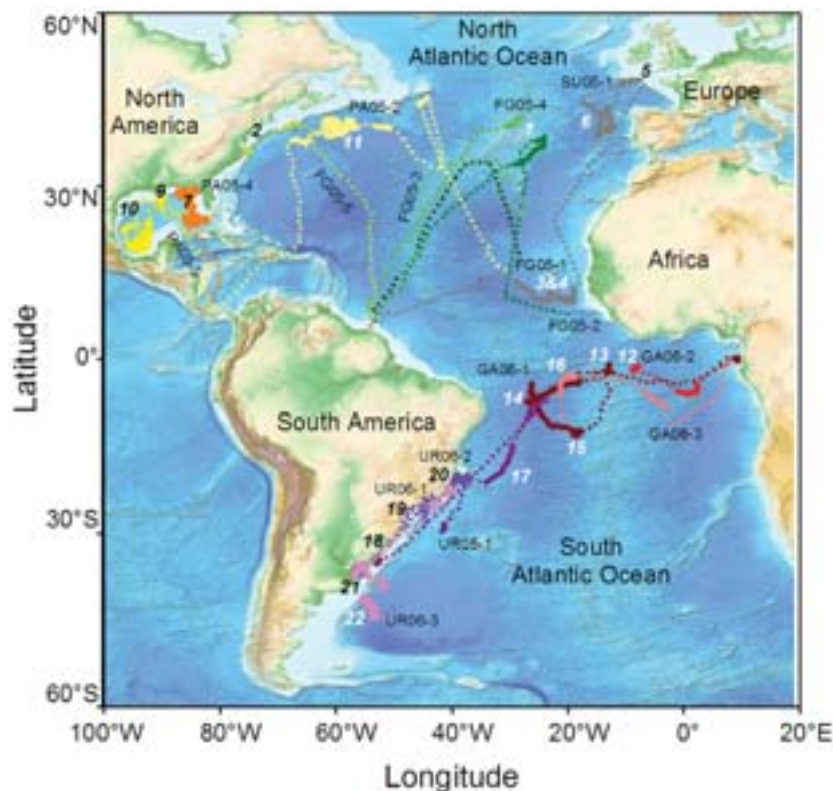


Figure 1. Movements of 16 leatherback turtles. Reconstructed movements of 16 Argos-tracked leatherback turtles during their migration in the Atlantic Ocean from 2005 to 2008. Twelve SRDLs were deployed on gravid females nesting in Panama ($n=3$, PAyear-ID), Suriname and French Guiana complex ($n=6$, SUyear-ID and FGyear-ID, respectively), and Gabon ($n=3$, GAYear-ID). Four others were deployed on leatherback turtles incidentally captured by Uruguayan fisheries (pelagic longlines and coastal bottom-set gillnets) in international waters of the Southwest Atlantic and in Kiyú, Uruguay, respectively (URyear-ID). For each turtle, transit and Temporary Residence Areas (TRAs) are identified by dotted and solid lines, respectively. Each TRA is identified by a number in black and white, for neritic and oceanic domains, respectively (see M&M for details). doi:10.1371/journal.pone.0013908.g001

2007. The third turtle (PA05-2) reached the Gulf Stream in October 2005 after crossing the Caribbean Sea. She remained in this oceanic area (between 36°N–42°N and 69°W–50°W, TRA11) during five months, before migrating southeast by March 2006 towards the Cape Verde Islands.

Gabon. The three turtles which left Gabon in March 2006 (GA06-1, GA06-2 and GA06-3), dispersed in the South Atlantic and remained within the South Equatorial Current between 0° and 13°S. Tracking of turtle GA06-2 ended in June 2006 while she was still in the Gulf of Guinea at 1°S–8°W (TRA12). GA06-1 reached a first oceanic area (1°S–13°W, TRA13) by May 2006 (Fig. 2) where she remained during one month before moving westward to another oceanic area located between 8°S–4°S and 27°W–25°W (TRA14) where she spent three months (Aug–Nov 2006) before reaching a last oceanic area situated at 12°S–18°W (TRA15) where she remained two months (Jan–Feb 2007). She then returned north-eastward approximately to the same oceanic area where she was in June 2006 (TRA13) and spent one month there before transmission ceased. Turtle GA06-3 spent four months (Jul–Oct 2006) close to the equator (1°–4°S, TRA16), then moved to the same oceanic area where turtle GA06-1 (TRA15) was located between January and March 2007, just before transmission ceased.

Uruguay. All four turtles which were released after being incidentally captured in the open ocean off the Uruguayan coast

($n = 3$) and in coastal waters of the Rio de la Plata ($n = 1$) in June 2005, August and October 2006 dispersed within the South-western Atlantic. The turtle UR05-1 moved north-eastward, slowed down around 20°S–30°W (TRA17) and reached 6°S–24°W at the end of November 2005 where GA06-1 also remained between August and November 2006 (TRA14). After one month in this oceanic area, she moved back towards the Uruguayan continental shelf (TRA18) where she was last located in April 2006. The sub-adult UR06-1 remained in the Southern Brazilian Bight (between 23°S and 29°S, TRA19) during its entire tracking. The male UR06-2 first moved north-eastward until 21°S and spent September between the continental slope and the Victoria-Trinidad seamounts (TRA20). He then travelled back along the continental shelf and reached the Rio de la Plata estuary (TRA21) in November 2006 where he remained until transmission stopped in March 2007. The turtle UR06-3 left the Uruguayan continental shelf in November 2006 and reached the Brazil-Malvinas Confluence area (TRA22) where she remained for two months (Dec 2006–Jan 2007). She came back to the Rio de la Plata estuary (TRA21) in early March 2007 where she stayed for three months (Fig. 2). Then she moved north-eastward along the Uruguayan and Brazilian continental shelves. From August 2007 to September 2007, she remained close to the Victoria-Trinidad seamounts and the continental slope (TRA20). She returned to the Rio de la Plata (TRA21) in January 2008 (Fig. 2). After spending

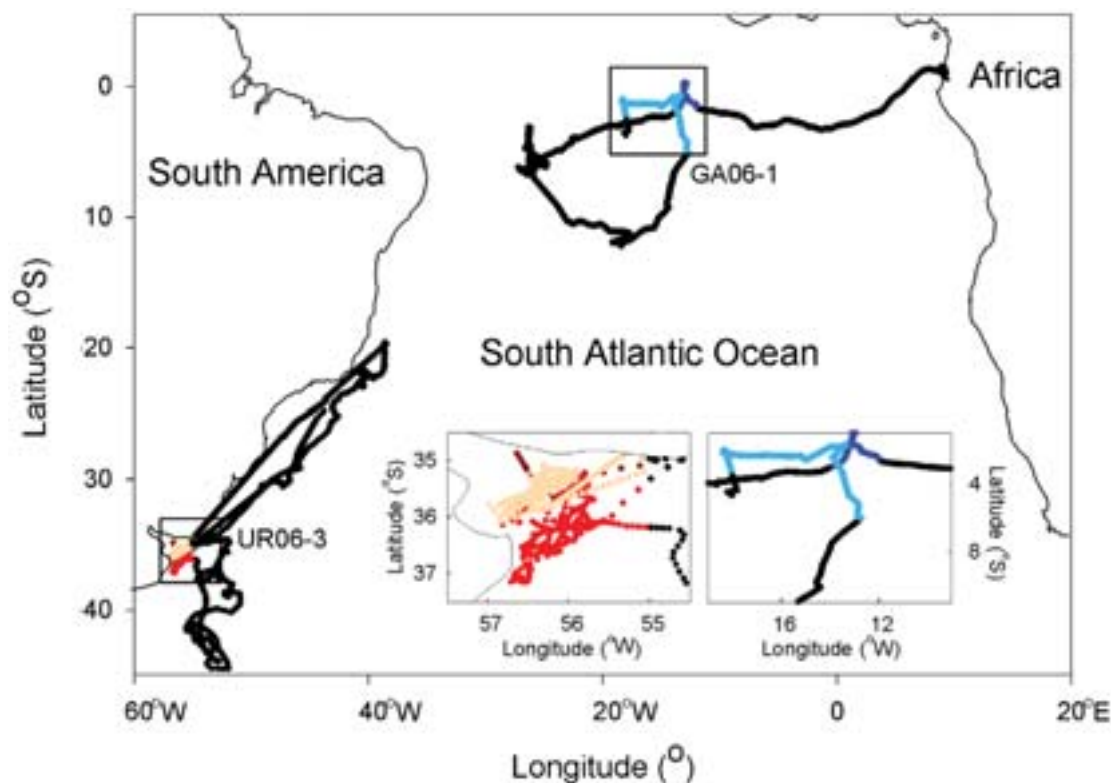


Figure 2. Fidelity to Temporary Residence Areas. Illustrative examples of fidelity to Temporary Residence Areas (TRAs) in leatherback turtles during their pluri-annual migration. After nesting in Gabon in March 2006, GA06-1 reached a first oceanic TRA (TRA13) by May 2006 (right insert, dark blue track) that she reached again by May 2007 (light blue track) after a counter-clockwise long loop in the middle South-equatorial Atlantic. After being released in the Rio de la Plata estuary in October 2006 (left insert, brown track), UR06-3 moved southward into oceanic water before coming back to her neritic TRA: the Rio de la Plata estuary (TRA21) by February 2007 (red track) that she reached again by January 2008 (orange track) after migrating north toward Brazilian waters close to the Victoria-Trinidad seamount chain. Each year, UR06-3 resided during 3 months in the Rio de la Plata estuary (TRA21).

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>4 months in the estuary, she headed northeast towards tropical waters before transmissions ceased in July 2008.

Drifter trajectories

Buoys travelling off the French Guiana-Suriname coasts have been shown to drift in different directions (**Fig. 3**). First, northwest towards the North American coasts (B1) and then possibly drift into the Gulf Stream until they reach the Azores (B2). From the Azores, the buoys can travel northward to the Irish Sea and the Bay of Biscay (B3), eastward to the Iberian coasts (B4), or southward to the Cape Verde islands, *via* the Canaries Islands (B5). Secondly, buoys can travel broadly northward to the Gulf Stream area (B6 and B7) and then drift to the east (B2). Last, they can travel eastward to the African coasts reaching the Guinea Dome area (B8 and B9). Buoys travelling off the Panama coasts (**Fig. 3**) can travel first northward to the Gulf of Mexico, and then possibly disperse either to the east (B10) or to the west into the Gulf (B11) or travel eastward by drifting into the Gulf Stream (B2). Buoys travelling off the Gabon coasts (**Fig. 3**) can travel westward into the South Atlantic Gyre (B12), from where they can end up on the South American continental shelf (B13), they can then travel south-eastward along the Brazilian coasts (B13). Buoys travelling off the Uruguay coasts (**Fig. 3**) can travel southward to the Brazil-Malvinas confluence area (B14). Although such data should be taken with caution as they were collected at different periods, they suggest that passive objects may drift from our different tagging sites and reach all the leatherback TRAs identified in this study, in approximately 1 to 3 years.

Environmental characteristics of temporary residence areas

For two turtles (FG05-1 and FG05-3) no temporary residence areas were identified possibly due to the relatively short duration of their tracks (<4 months) and/or the low quality of the data towards the end of the tracks. For the 14 remaining turtles, TRAs were located both in the neritic (e.g. TRA7, 10, 21 **Figs. 1, 2**) and the oceanic zone (e.g. TRA1, 11, 13; **Figs. 1, 2**) and were characterised by a high diversity of oceanographic conditions. Amongst the neritic TRAs, one (TRA21) was located in the estuary of the Rio de la Plata characterised by a high chlorophyll *a* surface concentration whereas others (e.g. TRA2, 7, 10) were located on the edge of continental shelves with a steep slope. Amongst oceanic TRAs, two were located in highly dynamic areas characterised by important mesoscale eddy activity: the Gulf Stream (TRA11, **Fig. 4a**) and the Brazil/Malvinas Confluence (TRA22), others were located in the Azores Current (TRA1), the Guinea Dome area (TRA3) and the South Equatorial Current (TRA12, 13, 16) characterised by oceanic fronts clearly highlighted in maps of absolute dynamic topography (MADT, **Fig. 4b**). All TRAs of Gabonese turtles were situated in the South Equatorial Current characterised by high chlorophyll *a* surface concentrations (**Fig. 4c**).

From the nesting site to the first temporary residence area

All turtles satellite-tagged on their nesting beach reached their first TRA after 21 to 99 days of transit with a high mean swimming and apparent velocities (typically $>45 \text{ cm.s}^{-1}$, i.e.

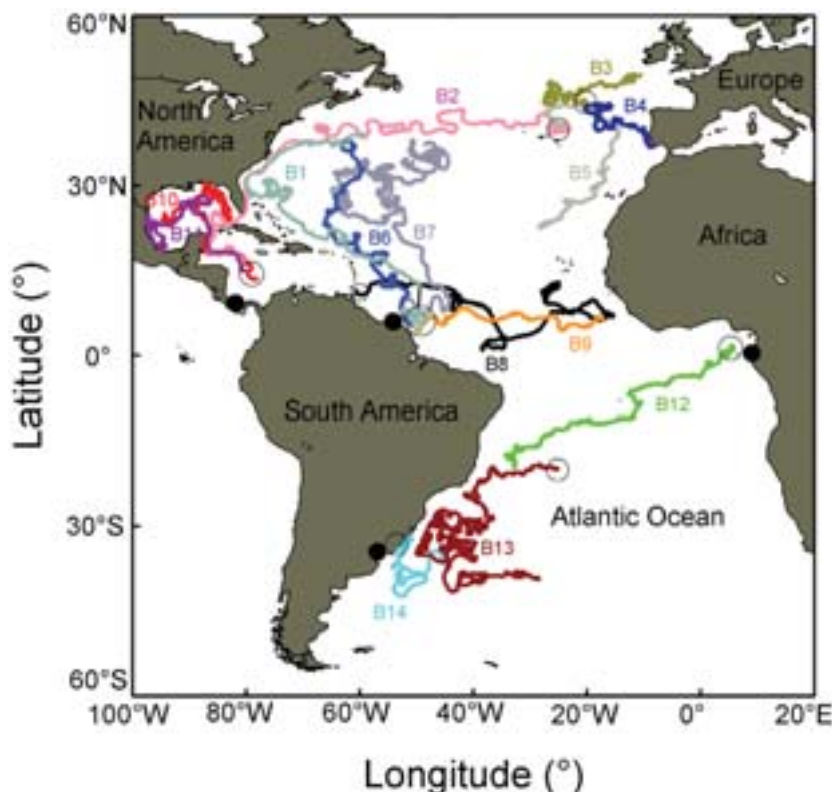


Figure 3. Trajectories for satellite-tracked drifters. Map of trajectories for satellite-tracked drifters released in the vicinity of leatherback turtle tagging sites. Filled circles show the location of the tagging sites. Dotted circles show the starting point of the drifter tracks. Drifters were selected to indicate possible drift scenarios from the tagging sites (Panama, Suriname, French Guiana, Gabon and International waters off the Uruguayan coasts) to the main Temporary Residence Areas of the leatherback turtles identified in this study. doi:10.1371/journal.pone.0013908.g003

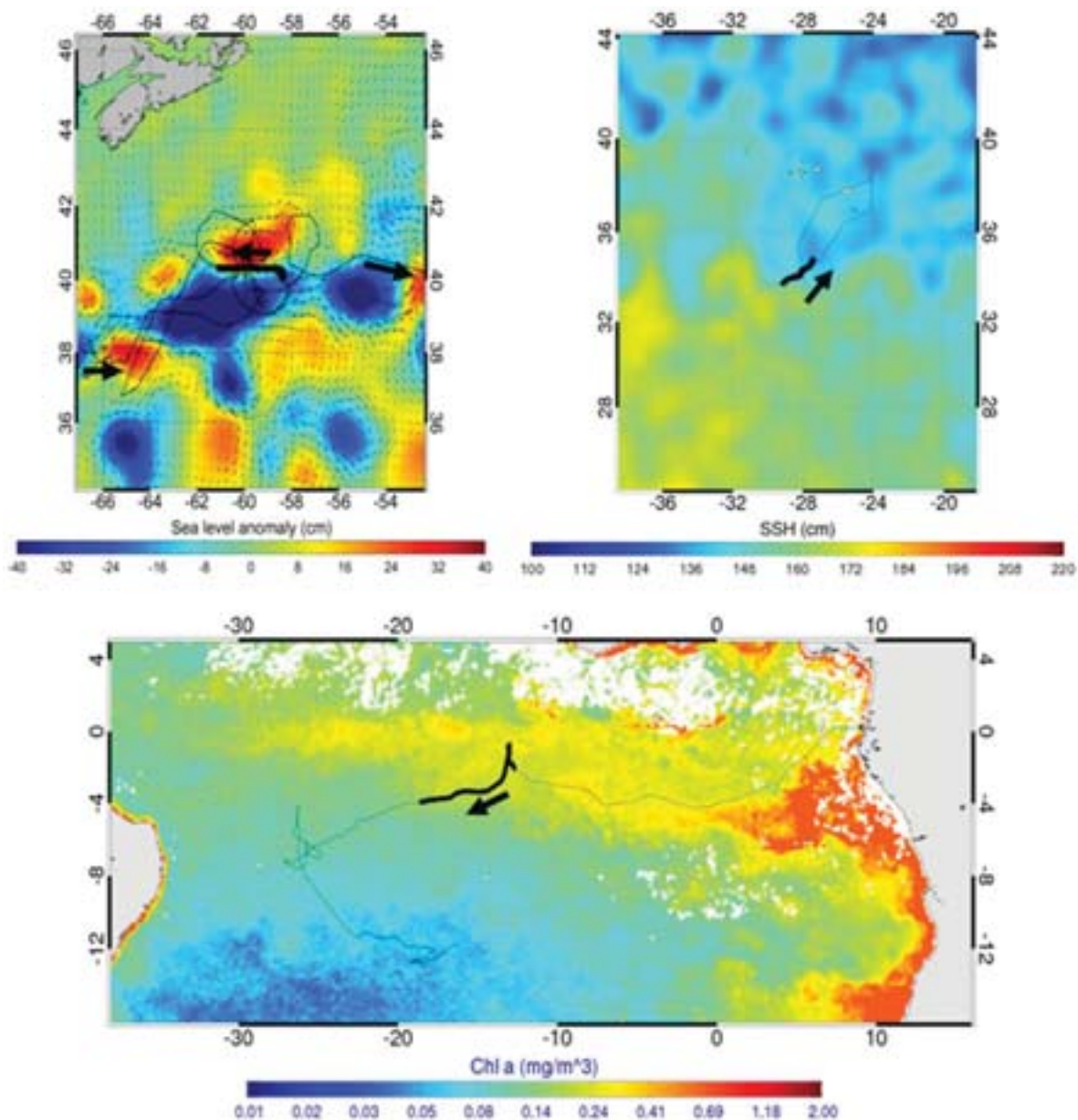


Figure 4. Migration paths and oceanographic parameters. a- Migration path in relation to weekly sea level anomaly (MSLA) of an Argos-tracked leatherback turtle (PA05-2) nesting in Panama in July 2005. The fine line represents the turtle's track from 10/10/2005 to 20/02/2006 (TRA11), while the bold line represents the week from the 30/12/2005 to the 06/01/2006 concurrent to MSLA map. b- Migration path in relation to weekly absolute dynamic topography (MADT) of an Argos-tracked leatherback turtle (FG05-2) nesting in French Guiana in July 2005. The fine line represents the turtle's track from 01/10/2005 to 24/02/2006 while the bold line represents the week from the 25/10/2005 to the 01/11/2005 (TRA 1) concurrent to MADT map. c- Migration path in relation to chlorophyll a surface concentration of an Argos-tracked leatherback turtle (GA06-1) nesting in Gabon in March 2006. The fine line represents the turtle's track from 04/03/2006 to 21/02/2007 while the bold line represents the period from the 01/06/2006 to the 30/06/2006 (TRA 13) concurrent to [Chla] map.
doi:10.1371/journal.pone.0013908.g004

39 km.day⁻¹, except GA06-3, **Table S1, Fig. 5**) and a high mean straightness index of the motor and apparent paths (mean *D/L* typically >0.8). Turtles from Suriname/French Guiana and Panama performed long and deep dives (typically >20 min and >80 m respectively, **Table S1, Fig. 5**), although spending on average half of their time between 0–10 m deep (**Table S1**). Turtles from Gabon spent a lower percentage of time between 0–10 m deep compared to other turtles and performed shallower dives (**Table S1**).

From transit areas to temporary residence areas

As turtles reached a TRA, there were marked changes in their vertical and/or horizontal behaviour depending on the type of habitat they exploited.

The passage from a neritic transit area to a neritic TRA (FG05-5, PA05-5, UR06-2, UR06-3) was associated with a decrease in swimming velocity (Kruskal-Wallis followed by a post-hoc Bonferroni test, $p < 0.05$ in all cases, **Table S1, Fig. 5**) and in the mean straightness index for the motor path while dive

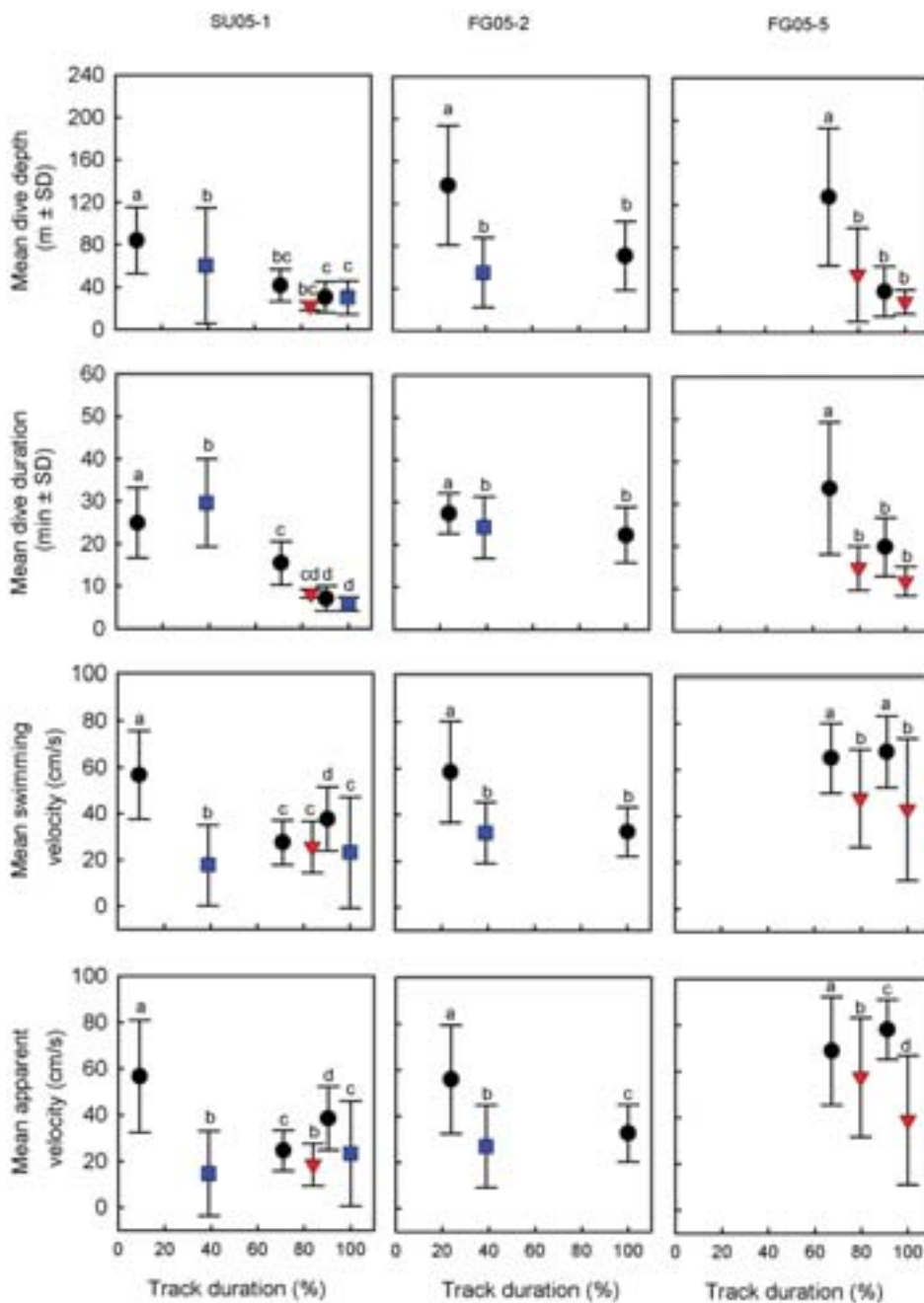


Figure 5. Variation in diving behaviour and velocities between areas. Diving behaviour and velocities in transit areas (filled dots), oceanic TRAs (filled crossed squares) and neritic TRAs (filled crossed triangles) for three Argos-tracked leatherback turtles nesting in Suriname (SU05-1) and French Guiana (FG05-2 and FG05-5) during their migrations in 2005. Differences between track sections were statistically tested using Kruskal-Wallis test followed by a post-hoc Bonferroni test. Different letters indicate significant ($p < 0.05$) differences among areas. Values are expressed as mean \pm SD. doi:10.1371/journal.pone.0013908.g005

parameters remained similar except for UR06-2 and UR06-3 for which dive depth decreased.

The passage from an oceanic transit area to a neritic TRA (FG05-5, SU05-1, PA05-4, PA05-5, UR05-1, UR06-2, UR06-3) was associated with a decrease in swimming velocity ($p < 0.05$ in all cases, except SU05-1, **Table S1, Fig. 5**), in the mean straightness index for the motor path and in dive depth ($p < 0.05$ in all cases, except SU05-1, **Table S1, Fig. 5**).

The passage from an oceanic transit area to an oceanic TRA (FG05-2, FG05-4, SU05-1, PA05-2, GA06-1, GA06-2, GA06-3, UR05-1, UR06-3) was associated with a decrease in swimming velocity ($p < 0.05$ in all cases, except UR06-3, **Table S1, Fig. 5**) while the change in straightness index was more variable. Dive depth decreased for all turtles when they reached their first oceanic TRA ($p < 0.05$ in all cases, **Table S1, Fig. 5**) except Gabonese turtles for which dive depth increased. However, when turtles

reached subsequent oceanic TRAs their diving patterns did not change.

The passage from a neritic transit area to an oceanic TRA occurred only once (PA05-4) and was associated with an increase in dive duration (**Table S1**).

Within neritic temporary residence areas

Within neritic TRAs, the mean swimming and apparent velocities were typically low ($<45 \text{ cm.s}^{-1}$, i.e. 39 km.day^{-1} , **Table S1, Fig. 5**) with a lower straightness index along the motor and apparent paths than before reaching the TRA (mean D/L typically <0.8). Within neritic TRAs, turtles spent a majority of their time in the upper water column with more than 40% of their time spent between 0–10 m (up to 69% for SU05-1, **Table S1**) while dives were typically shallow ($<50 \text{ m}$) and short ($<20 \text{ min}$, **Table S1, Fig. 5**). Turtles PA05-4 and PA05-5 as they mostly remained along the continental slope of the Gulf of Mexico performed deeper (between 60 and 140 m) and longer (typically $>20 \text{ min}$) dives. Compared to transit areas, the diving effort in term of total number of dives per hour increased regardless the initial domain (neritic or oceanic) they came from.

Within oceanic temporary residence areas

Within oceanic TRAs, mean swimming and apparent velocities were highly variable among individuals depending on the actual oceanic dynamics assessed through current velocity (**Table S1, Fig. 5**). Accordingly turtles showed variable spatial structure of their path (i.e. path straightness) while remaining within an oceanic TRA: (1) in fast-current TRAs such as the Brazil/Malvinas Confluence and the Gulf Stream, turtles UR06-3 and PA05-2 had relatively fast swimming and apparent velocities (typically $>45 \text{ cm.s}^{-1}$, i.e. 39 km.day^{-1}) but a relatively lower straightness index for both the motor and apparent paths (typically <0.8). (2) Yet, in similar fast-current oceanic TRAs such as the Loop Current, turtle PA05-4 showed a high straightness index for its motor path, a high swimming velocity opposite to the main current resulting in a slow apparent velocity and a low straightness index for the apparent path. (3) Conversely, in low-current oceanic TRAs, such as the South Equatorial Tropical Gyre, turtle UR05-1 showed low swimming and apparent velocities (typically $<30 \text{ cm.s}^{-1}$, i.e. 26 km.day^{-1}) but a high straightness index for both motor and apparent paths (typically >0.8) whereas turtles SU05-1, FG05-2 and FG05-4 showed a low straightness index for the motor path with similar low swimming and apparent velocities (typically $<35 \text{ cm.s}^{-1}$, i.e. 30 km.day^{-1}). (4) Finally, all three Gabonese turtles showed low apparent velocities (typically $<30 \text{ cm.s}^{-1}$, i.e. 26 km.day^{-1}) in the South Equatorial Tropical Gyre with either low (GA06-1) or high (GA06-2 and GA06-3) straightness index for the apparent paths.

Within oceanic TRAs, mean dive depth and mean dive duration were typically between 50–80 m (except UR06-3, **Table S1, Fig. 5**) and $>20 \text{ min}$ (except PA05-2 and UR06-3, **Table S1, Fig. 5**), respectively, with a high percentage of time spent between 0–10 m deep (typically $>50\%$, except PA05-4 and GA06-2, **Table S1**).

Discussion

For the last ten years, many studies have investigated in detail the diving behaviour and movements of leatherback turtles during their migration cycle in the Atlantic Ocean [19–21,24–35]. For instance, in the North Atlantic, Ferraroli et al. [19] and Hays et al. [29] tracked females from their nesting sites in French Guiana and Grenada, respectively, while James et al. [31,32] tracked male and

female leatherback turtles from an important foraging site in Nova Scotia. Evans et al. [26] described the migration patterns in the Gulf of Mexico of females nesting in Panama whereas in the South Atlantic, the recent study of López-Mendilaharsu et al. [20] focused on the behaviour of turtles captured in the Southwestern Atlantic Ocean. Yet to date, only one study concurrently investigated the migratory behaviour of leatherback turtles from both nesting and foraging sites in the North Atlantic basin [27]. The present study similarly brings together individual tracks but from three major nesting sites and one recently identified foraging area over the North and South Atlantic Ocean to identify temporary residence areas and associated environmental determinants. As such this study provides a new point of view on leatherback migration patterns and complements previously published works.

Atlantic migratory paths and TRAs

By monitoring 16 leatherback turtles from three nesting sites and one foraging area over the Atlantic ocean, this study clearly illustrates that the general dispersal patterns and TRAs used by the turtles may vary among individuals of a same nesting population and among populations. For instance females tracked from the nesting sites in French Guiana and Suriname only dispersed through the North Atlantic basin heading broadly northwest, northeast, or east (this study and [19,27]) whereas two of the three females tracked from their nesting beach in Panama dispersed in the Gulf of Mexico and the third one reached the Gulf Stream area (this study and [26]). To date, no satellite-tracked females from the Caribbean, French Guiana or Suriname nesting populations have ever entered the Gulf of Mexico or travelled south to the South Atlantic. In the Southern hemisphere, all three females tracked from Gabon dispersed through the South Atlantic basin mainly remaining within the South Equatorial Current while the turtles captured in coastal and oceanic waters off South America remained in the Southwestern Atlantic (this study and [20]). So within nesting populations, there is a tendency for migratory paths to be broadly similar (i.e. remaining within the same ocean body such as North Atlantic or Gulf of Mexico) but with large variation existing between the extreme paths taken (e.g. FG05-5 and FG05-3). Yet, there is a much greater variability of migratory paths between populations.

We identified 22 TRAs distributed throughout the Atlantic Ocean, 9 in the neritic domain and 13 in the oceanic domain. This corroborates previous studies suggesting that leatherback turtles are both oceanic and neritic foragers [20,25,40]. As a consequence, these TRAs did not share a common oceanographic determinant but on the contrary were associated with mesoscale surface oceanographic features of different types (i.e. altimetric features and/or surface chlorophyll *a* concentration). Several TRAs were located in distinct oceanic frontal zones and eddies. The importance of oceanographic fronts to this species, but also to marine birds and mammals (review in [41]) has already been described [19,24,34,42]. Other TRAs were located in estuaries and along coastal shelf breaks that constitute sharp water density discontinuities where biomass concentrates, including gelatinous zooplankton, the leatherback prey [43–45]. Slope waters seem indeed of important use for leatherback turtles. For instance, turtles PA05-4 and PA05-5 spent most of their time along the continental slope of the Gulf of Mexico, maybe foraging on gelatinous zooplankton aggregated along the shelf-break front [43]. All TRAs used by the turtles have been previously described as productive areas: e.g. the Mauritania upwelling [46], the Gulf of Mexico [47], the Gulf Stream [48], the Brazil/Malvinas Confluence [49], and the estuary of Rio de la Plata [50,51]

suggesting that TRAs may indeed be associated with foraging. In addition, several TRAs identified in this study closely match the high-foraging success areas previously identified for leatherback turtles during their pluri-annual migration in the North Atlantic [27]. Interestingly, individuals from a same nesting area may show contrasting patterns in habitat use such as PA05-5 only exploiting oceanic TRAs and PA05-2 only neritic ones. Migratory paths and habitat use patterns in the leatherback turtle thus are both characterized by high intra- and inter-population variation.

Vertical and horizontal behaviours within TRAs

Despite highly variable oceanographic conditions among TRAs, turtles interestingly rather exhibited relatively similar horizontal and vertical behaviours when in TRAs. First, when taking into account the influence of surface currents on the horizontal behaviour of the animals, it appears that, in general, turtles slowed down their swimming velocity as they reached TRAs and exhibited highly sinuous motor and apparent paths. This may be associated with area-restricted searching (ARS) patterns that other marine predators display when foraging [52–54]. However, in certain cases this general behaviour was shaped by local current conditions. This was revealed by the method used in this study which assesses the contribution of both the animal and the environmental cues to the way an animal remains in TRAs. For instance, within zones of high mesoscale activity (presence of many eddies) turtles rather increased their swimming velocities while performing sinuous movements to remain in the productive patch (e.g. turtles UR06-3 and PA05-2). An interesting case is the turtle PA05-4 that remained at the edge of the Loop Current for several months showing a highly sinuous apparent path and a low corresponding velocity but a straight motor path and high swimming velocity. This suggests that during several months, the turtle headed in a direction opposed to the Loop Current while she apparently remained in a restricted area looping within the flow. This behaviour might be an original strategy by which turtles feed at counter-current. Indeed, swimming at counter-current allows an animal to prospect water mass and thus potentially a prey patch without moving with respect to the sea bottom. Such behaviour may provide some benefits, as, for example, in terms of orientation by limiting extensive drifts throughout the oceanic basin, or in terms of foraging by maintaining the animal in an area where surface resources availability may be driven by deep, bathymetric-mediated, oceanic processes. This behaviour has been previously suggested for a leatherback turtle foraging in the Azores Current [37]. Different horizontal tactics seem thus to be used by the turtles to remain in a productive patch according to local oceanographic conditions. This highlights the necessity to cautiously interpret horizontal movement patterns in marine predators in relation to contemporaneous environmental dynamics [22,37]. Novel tracking technologies such as fastloc® GPS loggers by improving accuracy in tracking marine species [55] may help resolving the underlying patterns of movement in great details and allow a better understanding of relationships with environmental parameters.

Shallow diving behaviour was observed in all TRAs at all latitudes in a relatively homogenous way among individuals. In oceanic TRAs, dives were longer (>20 min) than in neritic TRAs and mainly concentrated in the epipelagic layer (50–80 m). This suggests that the diving behaviour was shaped by local prey distribution and density, as described for other marine vertebrates (e.g., [56,57]). Periods of very short shallow dives and high use of surface waters have previously been reported for leatherback turtles foraging at high latitude [24,28,33] where gelatinous plankton is available at shallow depths [58,59]. Similar pattern was described in basking sharks (*Cetorhinus maximus*) foraging on continental shelves [52,57]. Higher variability in diving behaviour

was observed in oceanic TRAs. Such variability in oceanic areas has also been observed in other marine species, particularly sea birds [60] and is likely driven by the stochastic nature of the oceanic environment resulting in less predictable and patchily distributed prey. This suggests that in neritic and geographically well-delimited TRAs, such as the Rio de la Plata estuary, where turtles exhibit relatively consistent diving patterns, spatio-temporal fishing regulations to mitigate bycatch may be more easily designed than in oceanic TRAs.

TRA fidelity and hatchling drift hypothesis

On one occasion, two individuals, one from the Southeast Atlantic and one from the Southwest Atlantic, stayed in the same TRA suggesting a potential connection between turtles from both sides of the South Atlantic. Leatherback turtles flipper-tagged on the beaches of Gabon have indeed previously been recovered in the waters of Argentina and Brazil [18] suggesting that turtles captured in international waters of the Southwest Atlantic likely belong to the West African nesting populations. Among the 16 turtles tracked in this study, several of them showed strong fidelity to TRAs (Fig. 2). Fidelity to a specific area has already been described in leatherback turtles foraging in Nova Scotia and in the Rio de la Plata estuary [20,32] but also in other sea turtle species [61]. Such behaviour is counterintuitive considering the high variability in post-breeding migration destinations observed among turtles of a given nesting population or among nesting populations. Yet, both may be linked to initial hatchling drift patterns [16,17]. The possible drift scenarios of hatchling turtles dispersing from their nesting sites may be inferred by looking at passive drifter trajectories. Here most of the individual dispersal patterns observed in the North Atlantic, the South Atlantic and the Gulf of Mexico showed interesting similarities with the trajectories of some satellite-tracked drifters (Figs 1, 3), although such data should be taken with caution as they were collected at different periods. In addition, most of the TRAs used by adult turtles during their post-breeding migrations were located along the drifter trajectories corroborating the “hatchling drift scenario” hypothesis [16]. Indeed, it has been suggested that hatchling turtles may imprint on several possible future and predictable foraging sites during the years when they are passively carried by ocean currents. Then, as adults they may make the decision to go to the preferred site(s) based on that initial experience and may follow the same routes [16,17]. Clearly, not all hatchling drift patterns generate possible scenarios for adult migration because of differential mortality rate between oceanographic areas (Gaspar et al. submitted). In addition, not all adult migration patterns match a hatchling drift scenario. For instance, in this study, some females left French Guiana and crossed the North Atlantic Gyre in a southwest-northeast direction heading towards the Azores. In this area, ocean currents are very weak and such trajectory could not occur by passive drift. Many other drifter trajectories end up however around the Azores which indeed represent a TRA used by many turtles (this study and [24,27]). This suggests that adult leatherback turtles may return to specific sites previously explored in their early lives without, however, always following the same routes as hatchlings but rather use shortcuts.

Conclusion

Identification of habitat use and associated diving behaviour is the first step for effective conservation of marine vertebrates. In this study, 22 temporary residence areas that may correspond to foraging areas have been identified in contrasted oceanographic environments ranging from neritic to oceanic domains for 16 Atlantic leatherback turtles. The observed migratory paths and

TRAs distributions appear to be related to multiple oceanographic conditions, and may be linked with initial hatchling drift scenarios [16]. This study thus highlights the importance but also the difficulty of implementing spatio-temporal fishing regulations over a large geographical scale and suggests that modification of fishing gears and fishing behaviours might be more efficient to protect such highly migratory species. Despite the sample size and diversity of study sites used in this study, it also appears that a larger multi-year dataset (at least >100 individuals) is needed through international collaborative efforts for providing general recommendations in terms of conservation of this critically-endangered species.

Supporting Information

Table S1 Summary of diving behaviour, swimming/apparent/current velocities and time spent in transit area/temporary residence area (TRA)/inter-TRA in oceanic (O) or neritic (N) domains in 16 Argos tracked leatherback turtles during their migration between 2005 and 2008 (see Fig. 1). Transit areas correspond to the time turtles spent from their nesting beach to their first TRA. TRAs correspond to $1^\circ \times 1^\circ$ areas where turtles spent more than 90 hours. Inter-TRAs correspond to the time turtles spent between two TRAs (see M&M for details). * for PA05-2, the 35 days at the end of the track were not taken into account due to the very few numbers of locations obtained during this period. Differences between areas were statistically tested using Kruskal-Wallis test followed by a post-hoc Bonferroni test. Different letters indicate significant ($p < 0.05$) differences among areas. Values are expressed as mean \pm SD.

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Author Contributions

Conceived and designed the experiments: SF CG MLM PM AD DE LK LP SV JYG. Performed the experiments: SF MLM PM AD DE LK VP LP SV JYG. Analyzed the data: SF CG PG. Contributed reagents/materials/analysis tools: CG MLM PM AD DE LK VP LP SV PG. Wrote the paper: SF CG JYG. Contributed to the first draft and to the corrections of the manuscript: MLM PM AD DE LK VP LP SV PG.

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**Analyses statistiques des résultats préliminaires
présentés dans la Partie 3, Section 3.2.**

Les liens entre les paramètres de migrations, i.e. la durée et les conditions environnementales (ici l'indice d'oscillation Nord Atlantique, NAO, **voir Partie 2**), la performance reproductrice et la masse corporelle des femelles ont été abordés grâce au suivi longitudinal de 27 femelles s'étendant sur trois reproductions successives de 2006 à 2011 (détail dans le tableau ci-dessous).

Saison 1 (S1)	Saison 2 (S2)	Saison 3 (S3)	N	RI S1S2	RI S2S3
2006	2008	2010	15	2 ans	2 ans
2006	2008	2011	4	2 ans	3 ans
2006	2009	2011	8	3 ans	2 ans

Nous avons considéré la masse corporelle maternelle en début de chaque saison de reproduction. La performance reproductrice des femelles est exprimée en nombre d'œufs total pondus par saison de ponte, et a été calculé pour chaque individu de la manière suivante : Nb œufs/saison = Moyenne nb œufs/ponte * Nb pontes/saison. Enfin, l'indice NAO a été moyenné sur le ou les deux premier(s) hivers (i.e. pour les migrations de 2 ans ou 3 ans, respectivement) pour chaque migrations réalisées par les individus à partir des indice NAO mensuels disponibles sur <http://www.cpc.ncep.noaa.gov/data/teledoc/telecontents.html> conseillé par Stenseth *et al.* 2003. En effet, on considère que les conditions trophiques (à la base du réseau trophique) rencontrées lors du printemps dépendent de l'indice NAO des mois d'hiver (Décembre à Mars) qui a précédé (Attrill *et al.* 2007).

Dans un premier temps, nous avons cherché à comprendre :

- si la performance reproductrice à une saison de ponte donnée pouvait expliquer la durée de la migration suivante (modèle 1),
- si la performance de reproduction réalisée à une saison de ponte donnée pouvait être expliquée par la durée et/ou l'indice NAO moyen associé(e) à la migration qui a précédée (modèle 2),
- si la masse corporelle maternelle au début d'une saison de ponte donnée pouvait être expliquée par la durée et/ou l'indice NAO moyen associé(e) à la migration qui a précédée (modèle 3).

Puis, nous avons cherché à comprendre si la variation de masse corporelle des femelles entre deux saisons de ponte successives pouvait être expliquée par les paramètres de la migration (durée, indice NAO) séparant les deux saisons (modèle 4).

Les relations possibles entre les paramètres de migrations, la masse et la performance reproductrice des femelles ont été examinés grâce à des modèles mixtes, où l'individu et la saison de ponte ont été considérés en tant que facteurs aléatoires, de sorte que la répétabilité des données soit prise en compte. A partir de chaque modèle complet, les variables explicatives ont été retirées une à une, et le modèle dont l'AIC était le plus faible a été sélectionné. De plus, pour les modèles 1, 2 et 3 tous les paramètres ont été standardisés de sorte que, s'il y a lieu, les coefficients associés aux différents paramètres soient comparables entre eux. Lorsque la masse corporelle maternelle était considérée en tant que variable à expliquer, la masse corporelle des femelles au début de la saison précédente a été considérée en covariable (modèles 3 et 4).

Les résidus des différents modèles présentaient une distribution normale. L'ensemble des analyses statistiques ont été réalisé avec le logiciel R 2.10.

**Reproductive synchrony
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Reproductive synchrony in a recovering bottlenecked sea turtle population

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Summary

1. The assessment of species extinction risk has been well established for some time now. Assessing the potential for recovery in endangered species is however much more challenging, because complementary approaches are required to detect reliable signals of positive trends.

2. This study combines genetics, demography and behavioural data at three different time-scales to assess historical and recent population changes and evidence of reproductive synchrony in a small population of olive ridley sea turtle *Lepidochelys olivacea*. *Lepidochelys* is considered as the most extraordinary example of reproductive synchrony in reptiles, yet to date, it has only been reported in large populations.

3. Using Bayesian coalescent-based models on microsatellite nuclear DNA variability, we demonstrate that effective population size in olive ridleys nesting in French Guiana has dramatically declined by 99% over the last 20 centuries. This low current population size is further illustrated by the absence of genetic mitochondrial DNA diversity in the present nesting population. Yet, monitoring of nesting sites in French Guiana suggests a possible recovery of the population over the last decade.

4. Satellite telemetry shows that over the first 14 days of their 28-days inter-nesting interval, i.e. when eggs maturation is likely to occur, gravid females disperse over the continental shelf. They then gather together with a striking spatiotemporal consistency close to the nesting site, where they later emerge for their second nesting event.

5. Our results therefore suggest that reproductive synchrony also occurs in small populations. Olive ridleys may ensure this synchrony by adjusting the duration of the second half of their inter-nesting interval prior to landing, possibly through social mediation.

6. Such reproductive synchrony may be related to the maintenance of some species-specific strategy despite former collapse and may contribute to the present population recovery. The gregarious behaviour of reproductive individuals close to shore where human-induced perturbations occur is however a cause for conservation concern for this still poorly known species.

Key-words: population history, population recovery, reproductive synchrony, satellite tracking, sea turtles

Introduction

Amongst life-history traits, reproductive synchrony (Darling 1938) is an important reproductive strategy that contributes

to population dynamics and species resilience. Reproductive synchrony is the process by which certain plants and animals time their reproduction to be temporally more clustered than would have been explained by environmental seasonality alone (for review see Ims 1990). Reproductive synchrony may occur at different times of the breeding cycle, from gametogenesis to parturition, and is expected to allow populations to persist and grow under environmental and demographic conditions that would otherwise make it impossible

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(Henson, Cushing & Hayward 2011). Previous studies have focused on the proximate factors acting as cues to maintain synchronous breeding within a population, and on the ultimate factors that act as selective forces giving survival values to the adaptation. There is a considerable variation in the degree of synchrony amongst species, and the complex mechanisms underlying this phenomenon are still not fully understood.

So far, three main types of proximate causes for reproductive synchrony have been proposed (review in Ims 1990): environmental cues directly connected to climatic seasonality (e.g. photoperiod, temperature, humidity, food availability, lunar and tidal rhythms); internal cues from the organisms' own endogenous rhythms (i.e. biological clocks); and social cues based on the exchange of signals between individuals within a population. Early studies of reproductive synchrony in colonially nesting birds led to the hypothesis that this behaviour had evolved through reduced risks of predation to individual offspring (Darling 1938). The most widely proposed mechanism for this predator hypothesis is predation dilution by which an individual's risk of predation is reduced owing to lower probability of encountering predators through swamping (Ims 1990). This predator hypothesis has further been validated in numerous species, from corals to mammals (e.g. Gaillard *et al.* 1993; Hovel & Morgan 1997). However, synchronous reproduction is unlikely to have evolved solely in response to predation on offspring (Rutberg 1987). Indeed, synchrony within populations has also been proposed to result from the selection of parturition timing by individuals to produce offspring at the best time for ambient conditions, food and water supply for optimal survival, growth and recruitment (e.g. Rutberg 1987; Ogutu *et al.* 2010). Both predator and seasonality hypotheses may be not exclusive but rather operate over a gradient depending on the actual environmental and ecological contexts (Ims 1990). Further environmental cues may be involved in synchrony, the most widely reported being related to lunar rhythms (e.g. Hanafy *et al.* 2010). Reproductive synchrony may also be socially driven, as shown in mass-nesting marine olive ridley turtle *Lepidochelys olivacea* (Plotkin *et al.* 1997), birds (Henson, Cushing & Hayward 2011) and mammals (e.g. Berger 1992), where egg laying and/or ovulation synchrony increases with population density through pheromonal and/or olfactory cues. Reproductive synchrony may further affect operational sex ratio, extra-pair mating and paternity and ultimately may enhance total population size (e.g. Henson, Cushing & Hayward 2011).

Reproductive synchrony has mostly been investigated in species with parental care. Much less information is available about the mechanisms and adaptive values of synchronous nesting and hatching in species without parental care (but see Spencer, Thompson & Banks 2001 for the freshwater turtle *Emydura macquarii*, Colbert, Spencer & Janzen 2010 for the painted turtle *Chrysemys picta*, Plotkin 2007 for the olive ridley turtle). In the case of sea turtles, females lay eggs at night on tropical sandy beaches without any further care. Amongst sea turtles, the olive ridley turtle is one of the most

extraordinary examples of reproductive synchrony, also referred as *arribada* (Pritchard 1969). Hundreds to thousands of gravid females synchronously come ashore on tropical sandy beaches within a spatially limited area, for a very limited period of time, to lay eggs. *Arribada* have been suggested to result from group-coordinated responses to environmental conditions such as rainfall (Plotkin *et al.* 1997) and/or to hormonally driven physiological cues (Plotkin 2007). However, these hypotheses have not actually been tested. It has been suggested that *arribada* reduce adult female depredation ashore by predator satiation (Plotkin 2007). *Arribada* have also been suggested to enhance multiple mating with genetic benefits to both maternal and offspring fitness (Plotkin 2007), which may partially explain why the olive ridley turtle is considered to be the most abundant sea turtle world-wide (Spotila 2004).

Like other sea turtles, olive ridley turtles are however considered to be an endangered species on a world-wide basis. Sea turtles are emblematic of marine biodiversity erosion as they show some of the sharpest historical population declines (Lotze & Worm 2009), as evidenced by archaeological and historical records of human exploitation on sea turtles (McClenachan, Jackson & Newman 2006; Kennett *et al.* 2008), and by more recent demographic surveys of nesting activity (IUCN 2009 Red List). It is therefore critically important to have a sound knowledge of the historical population baseline, current population dynamics and current genetic structures of such endangered species to implement the appropriate conservation strategies. Genetic diversity is critical for the fitness and long-term survival of endangered species (Frankham 2005). In addition, genetic structure and demographic history need to be taken into account for successful conservation action plans (Lande 1988). Yet, recent demographic history has not been investigated in any small sea turtle population. Indeed, the complex reproductive biology of these species (Bowen & Karl 2007), further influenced by global change (Reece, Castoe & Parkinson 2005), has considerably complicated our understanding of their current population dynamics and genetic structures. Furthermore, reproduction and survival of sea turtles are both highly influenced by their ecology at sea, as recently evidenced by satellite telemetry and turtle–fishery interaction models (e.g. Ferraroli *et al.* 2004). Yet the links between individual behaviour at sea, nesting activity on land and expected population restoration have never been concurrently explored in any given sea turtle population.

In this study, we used an original approach based on three different time-scales combining genetic, demographic and behavioural data to investigate recent demographic history and population trend in a population of olive ridleys and examine the potential mechanisms involved in these trends. In this species, *arribada* were historically reported in the large populations in Mexico, Costa Rica, India, and to a lesser extent in Suriname, western Atlantic Ocean (Pritchard 1969). These populations have dramatically declined, mostly due to egg poaching and fisheries bycatch, even though some may have recently started recovering, such as in the Guianas

(Guiana, Suriname, French Guiana; Kelle, Gratiot & De Thoisy 2009). The Guianese olive ridley population is therefore considered now as the largest population in the Atlantic Ocean (Kelle, Gratiot & De Thoisy 2009) and is a case study for recent restoration in a population of marine vertebrates.

Materials and methods

GENETIC ANALYSES

Current genetic diversity of the population and demographic history were investigated using both mitochondrial and nuclear DNA variability. Skin samples were obtained from female olive ridley whilst nesting on beaches of Cayenne and Rémire-Montjoly (French Guiana) in 2006. Sequences ($N = 30$) of cytochrome *b* and control region (mitochondrial DNA) genes were obtained with primers GLUDG tRNA Glu and H THR8 (Shaffer, Meylan & McKnight 1997) and LCM15382 and H8791o (Lopez-Castro & Rocha-Olivares 2005), respectively, using the conditions defined by the authors. All sequences were deposited in the GenBank data base (accession numbers of cytochrome *b* sequences from FJ795374 to FJ795403; accession numbers of control region sequences from FJ795404 to FJ795433). Low diversities on the cytochrome *b* and control region sequences (see Results) precluded any further inference of past demographic investigations with mitochondrial markers.

Nuclear genetic variability was investigated using 11 nuclear microsatellite loci OR1, OR2, OR4, OR7, OR9, Ei8, OR11, OR14, OR16, OR18 and OR22, according to the conditions reported in Aggarwal *et al.* (2004, 2008) for 46 females. Haplotypic and nucleotide diversity in mitochondrial DNA were investigated with DNASP 4.20.2 (Rozas *et al.* 2003). As far as nuclear DNA is concerned, the Markov chain method was used to assess Hardy–Weinberg equilibrium and observed heterozygote excess of microsatellites (GENEPOP 1.2, Raymond & Rousset 1995); nucleotide diversity was calculated with FSTAT 2.9.3.2 (<http://www2.unil.ch/popgen/softwares/fstat.htm>). Absence of significant dropout, stuttering and null alleles was confirmed with MICRO-CHECKER 2.2.3. (Van Oosterhout *et al.* 2004; <http://www.microchecker.hull.ac.uk/>); absence of linkage disequilibrium amongst the 11 microsatellite loci was confirmed with GENEPOP 1.2. We used a Bayesian clustering approach (software STRUCTURE 2.3.1, Falush, Stephens & Pritchard 2007) to determine whether there was any hidden population structure that could falsely generate a signature of population collapse (Wakeley & Aliacar 2001). This method uses a Markov Chain Monte Carlo (MCMC) approach to group individuals into K ($K = 1$ from $K = 4$) populations based on their genotypes without prior information, using the admixture population model, 1 000 000 iterations, 500 000 burn-in replicates and five independent replicates per K value.

Markov Chain Monte Carlo simulations were used to estimate the posterior distribution of the genealogical history, including (i) mutational and coalescent events and (ii) a demographic parameter, including growth rate and time elapsed since expansion or decrease, to assess long-term changes in historical population size. LogCombiner and Tracer (BEAST 1.4.7, Drummond & Rambaut 2007) were used to obtain the ratio between ancestral and current population sizes by combining five runs (2×10^9 iterations each) performed with MSVAR0.4 (Storz & Beaumont 2002). Respective effective ancestral and current population sizes and time since collapse or expansion were obtained in a similar way, with MSVAR0.4 and MSVAR1.3 (Storz & Beaumont 2002). To assess adult population sizes, we used an effective population size/adult population size ratio of 0.08, as this

value is the mean of compiled ratios previously assessed in reptiles (Frankham 1995). A priori mutation rates of nuclear DNA ranged from 5.7×10^{-4} to 9.6×10^{-3} , as previously set in several marine turtle species (Fitzsimmons 1998). Generation time for olive ridley was set at 13 years (Zug, Chaloupka & Balazs 2006). Bottleneck populations can produce distinctive genetic signatures in expected heterozygosity (Cornuet & Luikart 1996). When a population experiences a reduction in its effective size, it generally develops excess gene diversity at neutral loci, because the rare alleles that were lost contributed little to the overall heterozygosity (Cornuet & Luikart 1996). We assessed the olive ridley population for a deficiency of low frequency allele classes using Sign and Wilcoxon tests, as implemented in the program BOTTLENECK (Cornuet & Luikart 1996) under the two-phase mutation model (TPM) with 95% single-step mutations.

NESTING ACTIVITY MONITORING

Nesting beaches at Cayenne/Rémire-Montjoly (French Guiana) were patrolled nightly from sunrise to sunset during the nesting season (early May to early September) from 2002 to 2010 to count individual nesting events and tracks. The Grubbs' test statistic (Snedecor & Cochran 1989) for the detection of outliers, based on median absolute deviation, was used to identify peaks of turtle landing from 2002 to 2008.

SATELLITE TELEMETRY

Ten olive ridley turtles ($N = 5$ in 2006 and $N = 5$ in 2007) were individually equipped with a Satellite Relay Data Logger (SRDL 9000X; Sea Marine Research Unit, SMRU, St Andrews, UK, <http://www.smru.st-and.ac.uk/>) whilst nesting on beaches at Cayenne/Rémire-Montjoly (French Guiana, $N = 9$) and Eilanti (Suriname, $N = 1$). SRDL units were glued on the highest scale of the carapace using two-component fast set epoxy. Location data were recovered from Collecte Localisation Satellites (<http://www.cls.fr>) before being processed using IKNOS TOOLBOX software (Tremblay, Robinson & Costa 2009). Saltwater switch data were used to identify haul-out events for defining the start and the end of the inter-nesting period (time between two consecutive nesting events). In addition, SRDLs provided 24-h summary statistics of diving behaviour: these statistics include mean \pm SD of dive duration (± 10 s) and dive depth (± 1 m) and were used to assess individual daily diving behaviour. SRDLs also recorded *in situ* water temperatures (± 0.1 °C).

Results

POPULATION GENETICS AND RECENT DEMOGRAPHIC HISTORY

We investigated the genetic diversity of the olive ridley population nesting in the Guianas with both mitochondrial and nuclear DNA markers. The control region (795 bp) had a nucleotide diversity $\theta = 0.00063 \pm 0.00002$ (mean \pm SD) and a haplotype diversity $h = 0.239 \pm 0.096$ for three identified haplotypes. Theta and h diversities of the cytochrome *b* (1144 bp) were nil, with only one haplotype observed. For nuclear DNA, simulations revealed that $K = 1$ ancestral population was the most likely (estimated Ln probability of data = -1378 , vs. -1418 for $K = 2$, -1456 for $K = 3$, -1500 for $K = 4$). Genetic diversity and

observed heterozygosity averaged over loci were 0.61 ± 0.20 and 0.62 ± 0.20 , respectively. The population showed a small ($F_{is} = -0.0075$) departure from the Hardy–Weinberg equilibrium ($P < 0.05$), although both Chakraborty & Jin (1992) and Brookfield (1996) methods did not reveal any significant deviation from panmixia.

The demographic parameters of the Guianese population were investigated using microsatellite variability (see Materials and methods). Significant excess gene diversity suggested a recent population decrease, although only the Sign test was significant ($P = 0.03$). Assessment of ancestral and current population sizes with MCMC simulations supported this result. The mean strength of the posterior distribution of the ratio between ancestral population size N_1 and current population size N_0 was $\log(N_0/N_1) = -2.085 \pm 0.156$ (linear population expansion model) and $\log(N_0/N_1) = -2.106 \pm 0.147$ (exponential population expansion model) (Fig. 1a). The posterior distribution of $\log(T)$, T being the time since the population collapsed, was 2.18 ± 0.30 , indicating that the decrease in the Guianese population occurred some 150 ± 10 generations ago, i.e. 1950 ± 130 years ago. The posterior distributions for $\log(N_1)$ and $\log(N_0)$ had very limited overlap of 4.37 ± 0.64 and 1.86 ± 0.35 for N_1 and N_0 , respectively (Fig. 1b).

BEACH PATROLLING AND CURRENT POPULATION TRENDS

The nesting activity of the present population was monitored from 2002 to 2010 by daily patrols of the beaches surrounding Cayenne, French Guiana. An average of 2015 ± 284 nests per year was reported (Fig. 2a). Importantly, current field data showed a significant increase in the number of nests per year (Spearman's correlation $R_s = 0.933$, $P < 0.001$, $N = 9$ years, Fig. 2a).

Daily beach patrols performed from 2002 to 2008 also revealed mass landings of nesting turtles with peaks of 104 ± 11 nests (overall mean, $N = 53$ peaks, range 17–335 nests per peak) within 2 ± 0 nights ($N = 53$ peaks, range 1–6 nights). The two largest landings occurred in 2008, when 302 and 319 females emerged in 1 and 2 nights, respectively (Fig. 2b).

SATELLITE TRACKING AND CURRENT AT-SEA BEHAVIOUR

After nesting, the 10 satellite-tracked olive ridley turtles left the beach for 28.5 ± 1.9 days (range 18.0 to 39.8 days, Fig. 3a; Table 1) but remained relatively close to the beach (mean maximum distance from the beach 18.4 ± 2.9 km, $N = 10$ turtles, range 23.8 to 73.8 km, Fig. 3b). A concurrent analysis of dispersion and diving patterns indicated that the inter-nesting period could be divided into two distinct periods. During the first half of the inter-nesting period (14.1 ± 0.6 days, $N = 10$ turtles), turtles dispersed from 17.3 ± 0.1 to 50.8 ± 0.6 km from the beach (overall mean 26.4 ± 3.3 km, $N = 10$ turtles). A wide range of diving

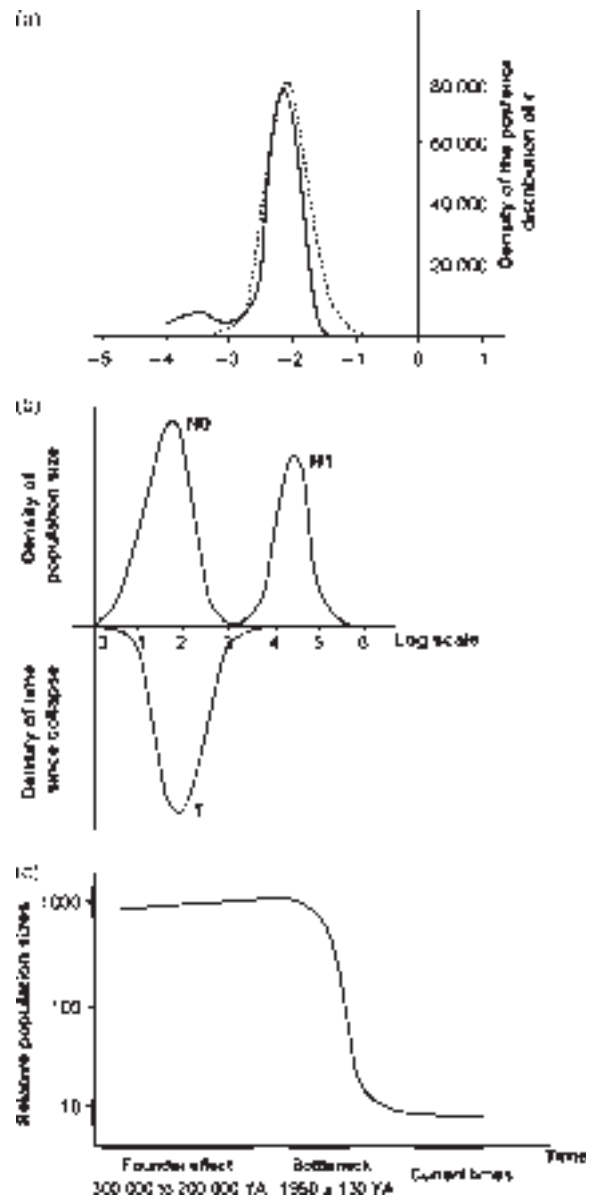


Fig. 1. Demographic history of the Guianese olive ridley population. (a) Population size change. Posterior distribution of $r = N_0/N_1$, representing the ratio on a logarithmic scale of present (N_0) to past (N_1) population sizes. Solid curve: exponential model of population size change; dash curve: linear model of population size change. (b) Past and present population sizes and time since the size has changed. Posterior distributions of past (N_1), current (N_0) and time since collapse (T , in generations). (c) Schematic demographic history of the Guianese olive ridley population. After a founder effect faced by their Atlantic ancestral stock that colonized the Atlantic 300 000–200 000 year ago (YA) (Bowen *et al.* 1998), the population faced a dramatic bottleneck (1950 ± 130 YA), resulting in a 130-fold decrease in the effective population size (this study).

behaviours was observed amongst individuals, with mean dive depths ranging from 6.8 to 37.9 m (overall mean 14.8 ± 3.0 m, overall max = 50 m, $N = 10$ turtles) with a mean dive duration of 24.9 to 64.1 min (overall mean 42.6 ± 4.4 min, overall max = 130 min, $N = 10$ turtles). During the second half of the inter-nesting period, all turtles

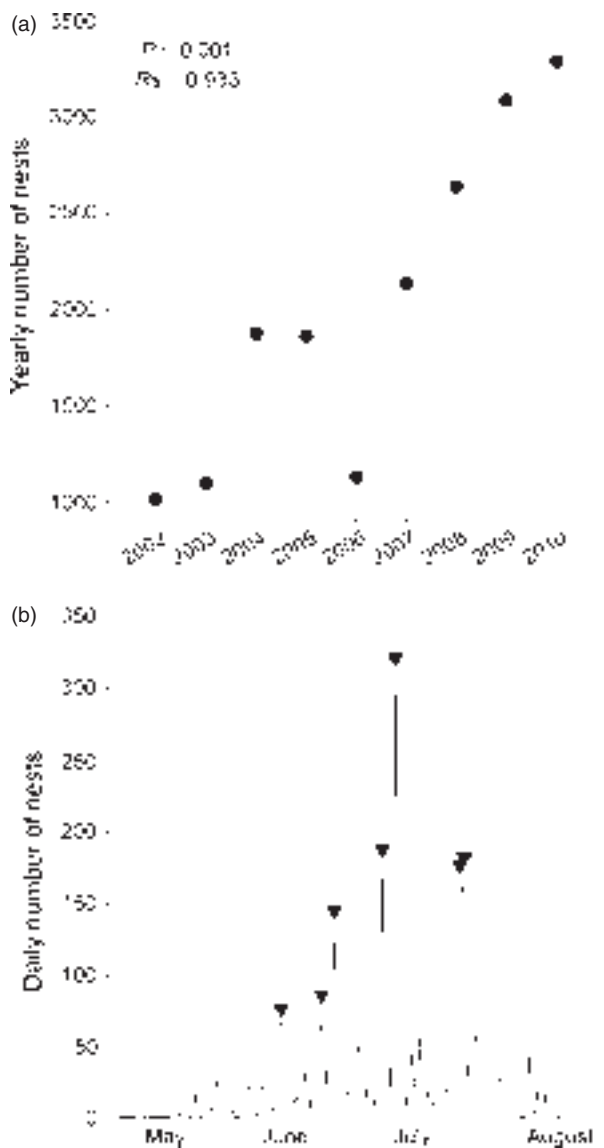


Fig. 2. Nesting activity of the population of olive ridley turtles on Cayenne beaches. (a) Recent annual trends. Yearly nesting activity of olive ridley has been increasing since 2002. (b) Daily nesting activity monitoring. Olive ridley females exhibit landing peaks (black triangle-down, identified by Grubbs' test), indicating an *arribada*-like behaviour (data 2008).

showed a striking consistency in their movements and diving patterns = (Fig. 3b–d). They all returned within very close vicinity of the departure beach (overall mean 8.7 ± 1.5 km, $N = 10$ turtles) in very shallow (< 12 m), relatively warmer waters (phase 1: 27.2 ± 0.1 vs. phase 2: 28.6 ± 0.1 °C; GLMM, with dive depth as covariate: $P < 0.001$, $F = 131.02$, $ddl = 1$). They then all ceased erratic diving in favour of sustained dives, which were systematically regular, constant, very shallow (overall mean 4.1 ± 0.3 m, range 3.4–6.5 m, $N = 10$ turtles) and short (overall mean 6.3 ± 0.9 min, range 3.6–11.6 min, $N = 10$ turtles). These dives differed significantly from those observed in the first phase (GEE_{depth}: $P < 0.001$, Wald $\chi^2 = 20.96$, $ddl = 1$; GEE_{duration}: $P < 0.001$, Wald $\chi^2 = 73.1$, $ddl = 1$). The

turtles returned ashore for their second nest at locations $c. 7.8 \pm 1.9$ km (range 2.9–23.9 km, $N = 10$ turtles) from the first nest.

CUES OF ARRIBADA-LIKE LANDING

There was a negative correlation between the duration of the first phase of the inter-nesting period and the mean water temperature experienced by the 10 satellite-tracked turtles during this phase ($R_S = 0.932$, $P < 0.001$, $N = 10$ turtles). However, no such relation was found during the second phase, or indeed over the entire inter-nesting period ($R_S = 0.04$, $R_S = 0.55$, respectively, $P > 0.05$ in both cases).

Discussion

Investigating historical population baseline, current population dynamics and genetics is critical for assessing population status, particularly in the case of critically endangered species. Major population declines have been reported in both terrestrial (e.g. Goossens *et al.* 2006) and marine vertebrates (e.g. Baker & Clapham 2004), including sea turtles (McClenachan, Jackson & Newman 2006; Kennett *et al.* 2008). However, understanding how severely depleted populations can recover has been proved to be much more challenging. This study investigates how a small population of sea turtles may be able to recover owing to its specific reproductive strategy, i.e. reproductive synchrony. This is to the best of our knowledge the first dedicated study based on a multidisciplinary approach at three different time-scales.

RECENT DEMOGRAPHIC HISTORY

Models using Bayesian coalescent-based approach of microsatellite nuclear DNA variability (Storz & Beaumont 2002) have recently allowed the investigation into recent population history in large endangered vertebrates (e.g. Goossens *et al.* 2006). Using similar Bayesian coalescent-based models of microsatellite nuclear DNA variability, our study suggests that the present population of olive ridley turtles nesting in Suriname and French Guiana originates from an ancestral population 130 times larger. This ancestral population may then have experienced a dramatic decline over the last 2000 years and now consists of a non-substructured population, as revealed by Hardy–Weinberg equilibrium. Our simulations suggest that the effective ancestral population was about 20 000 breeding animals, whilst the effective current population is estimated to be between 100 and 150 breeding animals. Simulations of the effective current population correspond to an estimated current population of 1250–1850 breeders. As the ratio of total/efficient population size is not set specifically to olive ridleys, this kind of interpolation should be considered with caution. However, these theoretical estimates correspond very well to our field data of 1343 females nesting yearly, when considering that olive ridley turtles produce on average 1.5 nests per breeding year

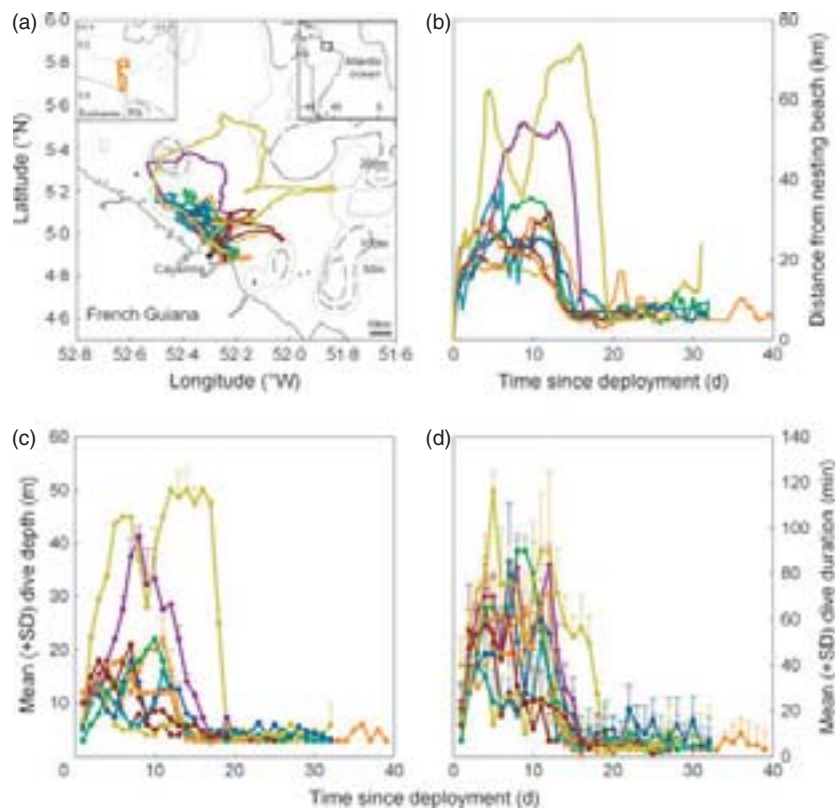


Fig. 3. At-sea ecology of 10 satellite-tracked olive ridley turtles during their inter-nesting period. (a) Reconstructed at-sea movements of olive ridley turtles nesting in French Guiana (FG) and Suriname (insert). The turtles remained in shallow coastal waters between two consecutive nesting events. (b) Distance travelled from the deployment site. The turtles dispersed during the first half of the inter-nesting period before remaining close to the nesting beach for the last 2 weeks spent at sea. (c, d) Diving behaviour, in terms of daily dive depth and duration. Vertical and horizontal patterns amongst individuals were consistent.

(Plotkin 2007), indicating that our simulation outputs are highly reliable.

The magnitude of this 130-fold population decline is similar to that reported in the Caribbean, where today's sea turtle populations (green turtle *Chelonia mydas*, hawksbill turtle *Eretmochelys imbricata*) represent only 0.3% (i.e. a 333-fold decline) of their historical abundance owing to human exploitation (McClenachan, Jackson & Newman 2006). Similar declines have been reported in populations of whales (99.9% decrease Baker & Clapham 2004), or orang-utans *Pongo pygmaeus* (95% decrease, Goossens *et al.* 2006) for instance, although these massive population collapses occurred over a shorter period of time. Amongst current species declines, the population collapse observed in the Guianese olive ridley is undeniably one of great magnitude.

The recent population decrease suggested by our results is further supported by the significant excess of gene diversity and particularly by the dramatically low level of mitochondrial genetic diversity in the observed control region compared to those reported in Pacific (Lopez-Castro & Rocha-Olivares 2005) and Indian olive ridley populations (Shanker *et al.* 2002; Aggarwal *et al.* 2008). Indeed, such a low DNA diversity may be attributed to two major demographic events: either a founder effect explained by a recent (300 000 years ago) colonization of the western Atlantic by

olive ridley turtles (Bowen *et al.* 1998) or an extensive and recent population collapse as suggested by our results (Fig. 1c). The mitochondrial mutation rate used in our study to estimate when this decline occurred is not specific to olive ridleys, yet it encompasses the range of values calculated for other marine turtles (Fitzsimmons 1998). Accordingly, the time-scale at which the population has been estimated to decline (i.e. during the last 2000 years) should be interpreted as first-order approximation. This is however consistent with archaeological records reporting local overexploitation, leading to the depletion of sea turtles (*Chelonidea*) in Mexico between *c.* 2300 and 5500 years ago (Kennett *et al.* 2008). This bottleneck may be related to human exploitation of sea turtles, both historically and more recently (McClenachan, Jackson & Newman 2006; Kennett *et al.* 2008). In the case of the Guianese olive ridley, it is more likely that the collapse observed within the last 2000 years was due to egg poaching and/or selective harvesting of nesting females during mass landing, rather than to more recent interactions with fisheries. Indeed, selective harvest (i.e. of a specific age and sex class) has been reported to drive population fluctuations (Bunnfeld *et al.* 2009). Dramatic environmental effects, which have yet to be identified, may also be linked to the decline in the Guianese olive ridley population.

Table 1. Summary of the horizontal and vertical behaviour during the inter-nesting interval of 10 satellite-tracked olive ridley turtles from French Guiana ($N = 9$) and Suriname ($N = 1^*$)

Turtle's ID	Entire inter-nesting interval (IP)										First phase of the inter-nesting interval (IP1)					Second phase of the inter-nesting interval (IP2)							
	Duration (days)	Water temperature (°C)	Distance from the beach (km); mean \pm SE; [max]		Dive depth (m); mean \pm SE; [max]		Dive duration (min); mean \pm SE; [max]		Duration (days)	Distance from the beach (km); mean \pm SE; [max]		Dive depth (m); mean \pm SE; [max]		Dive duration (min); mean \pm SE; [max]		Duration (days)	Distance from the beach (km); mean \pm SE; [max]		Dive depth (m); mean \pm SE; [max]		Dive duration (min); mean \pm SE; [max]		Distance between the 2 nests' sites
			mean \pm SE; [max]	SE; [max]	mean \pm SE; [max]	SE; [max]	mean \pm SE; [max]	SE; [max]		mean \pm SE; [max]	SE; [max]	mean \pm SE; [max]	SE; [max]	mean \pm SE; [max]	SE; [max]		mean \pm SE; [max]	SE; [max]					
A	27.0	27.0	12.9 \pm 0.2 [26.0]	6.0 \pm 0.7 [16.0]	16.5 \pm 3.4 [65.0]	13.9	18.9 \pm 0.2 [26.0]	8.2 \pm 1.1 [16.0]	27.2 \pm 5.0 [65.0]	5.0	6.5 \pm 0.1 [8.9]	3.6 \pm 0.1 [4.0]	4.9 \pm 0.5 [4.0]	13.2	7.3 \pm 0.1 [17.3]	3.7 \pm 0.2 [6.0]	4.9 \pm 0.5 [10.0]	24.1	7.0	4.9 \pm 0.5 [19.0]	5.3	5.7	
B	39.8	27.1	12.7 \pm 0.2 [30.6]	7.4 \pm 0.9 [22.0]	18.3 \pm 3.3 [70.0]	15.7	21.1 \pm 0.2 [30.6]	13.3 \pm 1.3 [22.0]	39.8 \pm 4.7 [70.0]	4.7	7.3 \pm 0.1 [20.2]	3.6 \pm 0.2 [6.0]	4.9 \pm 0.5 [19.0]	24.1	8.0 \pm 0.1 [23.9]	3.6 \pm 0.2 [6.0]	4.9 \pm 0.5 [19.0]	17.1	7.0	4.9 \pm 0.5 [19.0]	23.9	9.1	
C	31.0	27.0	12.2 \pm 0.3 [23.8]	4.9 \pm 0.5 [14.0]	13.7 \pm 2.2 [40.0]	13.9	17.3 \pm 0.1 [20.2]	6.8 \pm 0.8 [14.0]	24.9 \pm 2.7 [40.0]	7.0	17.3 \pm 0.3 [35.6]	12.4 \pm 1.6 [22.0]	29.0 \pm 2.7 [90.0]	18.1	6.7 \pm 0.1 [12.0]	3.4 \pm 0.1 [4.0]	5.5 \pm 0.7 [10.0]	18.1	7.0	3.6 \pm 0.6 [12.0]	9.1	9.7	
D	31.9	26.5	15.2 \pm 0.3 [35.6]	7.3 \pm 1.1 [22.0]	26.0 \pm 5.1 [90.0]	13.9	26.2 \pm 0.3 [35.6]	9.8 \pm 1.0 [22.0]	52.4 \pm 7.0 [90.0]	18.1	23.3 \pm 0.3 [39.4]	10.8 \pm 0.4 [18.0]	42.1 \pm 2.5 [85.0]	18.1	9.1 \pm 0.1 [24.5]	3.9 \pm 0.2 [6.0]	3.6 \pm 0.6 [12.0]	20.2	7.0	3.6 \pm 0.6 [12.0]	9.7	5.4	
E	32.0	27.3	14.3 \pm 0.2 [39.4]	6.1 \pm 0.6 [16.0]	15.0 \pm 2.2 [50.0]	11.8	21.8 \pm 0.2 [28.5]	10.8 \pm 0.4 [18.0]	42.1 \pm 2.5 [85.0]	18.2	39.3 \pm 0.6 [54.5]	24.1 \pm 1.4 [45.0]	56.5 \pm 2.7 [100.0]	4.1	7.0 \pm 0.1 [17.1]	4.6 \pm 0.2 [8.0]	10.4 \pm 1.0 [45.0]	18.2	4.1	11.6 \pm 2.3 [26.0]	2.9	6.5	
F	32.0	27.8	13.4 \pm 0.2 [28.5]	7.3 \pm 0.4 [18.0]	24.6 \pm 1.9 [85.0]	13.8	21.8 \pm 0.2 [28.5]	10.8 \pm 0.4 [18.0]	42.1 \pm 2.5 [85.0]	18.2	22.8 \pm 0.3 [32.0]	11.6 \pm 0.7 [22.0]	35.3 \pm 2.6 [85.0]	9.3	6.3 \pm 0.1 [7.4]	3.5 \pm 0.1 [6.0]	4.4 \pm 0.6 [20.0]	9.3	9.3	4.4 \pm 0.6 [20.0]	6.5	4.6	
G	18.0	26.3	35.4 \pm 0.6 [54.5]	20.4 \pm 1.4 [45.0]	47.0 \pm 3.1 [100.0]	13.9	39.3 \pm 0.6 [54.5]	24.1 \pm 1.4 [45.0]	56.5 \pm 2.7 [100.0]	4.1	22.7 \pm 0.2 [29.1]	13.5 \pm 0.5 [20.0]	55.1 \pm 3.3 [95.0]	8.3	21.7 \pm 1.3 [51.4]	6.5 \pm 1.0 [12.0]	11.6 \pm 2.3 [26.0]	4.1	8.3	11.6 \pm 2.3 [26.0]	2.9	4.6	
H	24.1	26.6	16.4 \pm 0.3 [54.5]	8.2 \pm 0.6 [22.0]	22.4 \pm 2.2 [85.0]	14.8	22.8 \pm 0.3 [32.0]	11.6 \pm 0.7 [22.0]	35.3 \pm 2.6 [85.0]	9.3	50.8 \pm 0.6 [73.8]	37.9 \pm 1.5 [50.0]	64.1 \pm 3.3 [130.0]	10.1	6.3 \pm 0.1 [48.3]	4.5 \pm 0.2 [6.0]	4.3 \pm 0.6 [6.0]	9.3	10.1	4.3 \pm 0.6 [6.0]	5.1	7.8 \pm 1.9	
I*	20.1	27.1	15.9 \pm 0.3 [29.2]	10.7 \pm 0.7 [20.0]	41.3 \pm 3.6 [95.0]	11.8	22.7 \pm 0.2 [29.1]	13.5 \pm 0.5 [20.0]	55.1 \pm 3.3 [95.0]	8.3	50.8 \pm 0.6 [73.8]	37.9 \pm 1.5 [50.0]	64.1 \pm 3.3 [130.0]	10.1	8.5 \pm 0.5 [48.3]	4.5 \pm 0.2 [6.0]	4.3 \pm 0.6 [6.0]	10.1	10.1	4.3 \pm 0.6 [6.0]	5.1	7.8 \pm 1.9	
J	28.0	26.2	35.5 \pm 0.7 [73.8]	27.1 \pm 1.9 [50.0]	45.0 \pm 3.6 [130.0]	17.9	50.8 \pm 0.6 [73.8]	37.9 \pm 1.5 [50.0]	64.1 \pm 3.3 [130.0]	10.1	14.1 \pm 0.6 [26.4]	14.8 \pm 3.0 [3.3]	42.6 \pm 4.4 [14.3]	2.0	8.7 \pm 1.5 [4.1]	4.1 \pm 0.3 [0.3]	6.3 \pm 0.9 [6.3]	10.1	10.1	6.3 \pm 0.9 [6.3]	5.1	7.8 \pm 1.9	
All	28.5 \pm 1.9	26.8 \pm 0.1	18.4 \pm 2.9	10.5 \pm 2.3	27.0 \pm 4.0	14.1 \pm 0.6	26.4 \pm 3.3	14.8 \pm 3.0	42.6 \pm 4.4	14.3 \pm 2.0	8.7 \pm 1.5	4.1 \pm 0.3	6.3 \pm 0.9	7.8 \pm 1.9	8.7 \pm 1.5	4.1 \pm 0.3	6.3 \pm 0.9	14.3 \pm 2.0	4.1 \pm 0.3	6.3 \pm 0.9	7.8 \pm 1.9	6.3 \pm 0.9	7.8 \pm 1.9

Dispersion and diving parameters are given for each individual (turtles' ID from A to J) during their entire inter-nesting interval (IP), and during the two phases of the inter-nesting periods (i.e. IP1 and IP2).

CURRENT OLIVE RIDLEY POPULATION TRENDS IN
GUIANAS AND WORLD-WIDE

Despite this relatively recent dramatic decline, the monitoring of nesting beaches in French Guiana reveals that the annual number of nests has increased from *c.* 1000 in 2002 to 3300 in 2010, with an average of 2015 nests per year, *i.e.* 1343 turtles nesting yearly. In sea turtles, where inter-annual variations in nesting numbers may reflect different remigration intervals, estimates of population trends over such a short period of time should be interpreted with caution (*e.g.* Hays 2000). However, as olive ridley turtles show a low variability in remigration intervals by nesting every 1 or 2 years (Plotkin 2007), we are confident that our results calculated over 10 years are good estimates of the actual trends of the Guiana's population. With three additional years of data, this study also supports the increase recently reported in the olive ridley nesting population in French Guiana (Kelle, Gratiot & De Thoisy 2009). Such an increase has been interpreted as a shift of nesting females from neighbouring Suriname to French Guiana rather than by recruitment of new breeders (Kelle, Gratiot & De Thoisy 2009). In southern neighbouring Brazil, da Silva *et al.* (2007) suggest that conservation efforts contributed to a 10-fold increase in nesting activity over the last 11 years, resulting in similar population size (2600 nests, *i.e.* *c.* 1700 breeding females in 2003). At-sea survey estimates of olive ridley abundance in the eastern tropical Pacific also suggest an increase in their population numbers (from *c.* 1.1 million in 1998 to 2.9 millions in 2006), which is consistent with the dramatic increase reported in olive ridley nesting populations over the last decade in Mexico and Costa Rica (see Eguchi *et al.* 2007). In contrast, the olive ridley nesting population in India, renowned for its massive *arribada*, is reported to have declined since 1994 mostly due to fishery-related mortality of adults (Shanker, Pandav & Choudhury 2003). Nevertheless, compared to these large nesting populations found in the Pacific and in India, the size of the Guianese population (1000–5000 effective breeders) even though increasing remains close to the critical level required to maintain long-term evolutionary potential (Lynch & Land 1998). This result suggests that efficiency of reproductive activity may therefore play a critical role in the recovery of this population.

PRESENT BEHAVIOURAL SYNCHRONY IN GUIANESE
OLIVE RIDLEYS

In French Guiana, olive ridley turtles show evidence of mass nesting similar to *arribada*, yet to a lesser extent than reported in some of the largest populations in Mexico and Costa Rica (Eguchi *et al.* 2007). First, daily beach patrolling showed that individuals emerge on land during peaks that may account for up to 11% and 12% of the annual nesting activity, and 30% and 32% of the estimated number of breeding females. Secondly, satellite tracking indicated that the mean duration of the inter-nesting interval of olive ridley turtles in the Gui-

anas is similar to inter-nesting intervals of mass-nesting olive ridley in Costa Rica (Plotkin *et al.* 1997; Plotkin 2007). This suggests that in this species, reproduction synchrony is not limited by population size, although mass landing occurs to a lesser extent in smaller populations.

Satellite-relayed behavioural data collected in this study provided further evidence of synchrony patterns during the inter-nesting interval. Until now, our knowledge of at-sea behaviour in olive ridley turtles prior to *arribada* was based on a unique direct observation in Costa Rica, where individuals were reported to gather and remain motionless on the seabed in shallow waters close to the shore (Plotkin, Polak & Owens 1991). Here, we show that gravid olive ridley turtles do not adopt such motionless behaviour during the entire inter-nesting interval. During the first half (14 days) of the 28-days inter-nesting interval, the turtles travelled a fairly long distance (up to 70 km) over the continental shelf whilst performing long (> 40 min) and deep (up to 50 m) dives. This pattern of long and deep dives is quite unlike the simple near-surface and repetitive diving conducted by animals that are simply travelling (*e.g.* Hays *et al.* 2001) and may rather be interpreted as benthic dives for either resting or foraging purposes (Hays *et al.* 1999; McMahan, Bradshaw & Hays 2007). Such active horizontal and vertical activity during the first phase of the inter-nesting interval is similar to that reported in the leatherback turtle *Dermochelys coriacea* during the nesting season in French Guiana (Fossette *et al.* 2007; Georges *et al.* 2007), which has been interpreted as foraging attempts (Fossette *et al.* 2008).

Several tracking studies in other sea turtle species have shown a common behaviour where breeding females decrease their dive duration in the few days preceding a nesting event (green turtles: Hays *et al.* 1999; hawksbill turtles: Houghton *et al.* 2008; leatherback turtles: Fossette *et al.* 2007; olive ridley turtles: Hamel, McMahan & Bradshaw 2008; this study). This may be related to the approach and selection of the nesting beach. However, the changes in behaviour we recorded are fundamentally different from these other observations, in that we showed a striking consistency across individuals in terms of horizontal and vertical movements, so that they all gathered together close inshore at the same time. Such dramatic behavioural changes strongly suggest a group-coordinated pattern, anticipating a mass landing event.

PROXIMATE CUES OF SYNCHRONY IN THE OLIVE RIDLEY
TURTLE

To date, environmental and social cues are the main factors considered to mediate *arribada* in the olive ridley turtle. *Arribada* have been suggested to occur at the end of heavy rainfall in Costa Rica, although this relationship has to be statistically validated (Plotkin *et al.* 1997). However, it is not clear yet how olive ridleys assess rainfall when at sea prior to landing. Moreover, rain rather affects sand humidity which in turn may affect embryonic development and hatching success in sea turtles (Kraemer & Bell 1980). Thus, more investigations are needed to understand the links between

rainfall and *arribada*, and its potential costs/benefits for olive ridley populations.

We found a negative relationship between the water temperature experienced by the turtles and the duration of the first half of the inter-nesting interval, but significance failed for the duration of the second half and for the entire inter-nesting interval. Consistent with the ectothermic physiology of sea turtles, previous studies have reported the inter-nesting interval to increase in cooler waters, with a mean raise from 10 to 25 days for water temperatures declining from 28 to 22 °C (Sato *et al.* 1998; Hays *et al.* 2002). If this relation holds for olive ridleys in French Guiana, where water temperature averages *c.* 27 °C (Table 1), female turtles would perform inter-nesting intervals of about 13 days. However, our results showed that in French Guiana, females performed inter-nesting intervals of 28 days, similar to those reported in olive ridleys nesting in *arribada* in Costa Rica (Plotkin 2007), yet with a first – thermal dependent – phase of 14 days. This suggests that the first half of the inter-nesting interval may be associated with temperature-dependent egg maturation, whereas the second half of the inter-nesting interval may be related to landing synchrony. Indeed, despite the fact that all satellite-tracked females showed a consistent two-phased behaviour at sea, some of them did not lay their first nest during a mass landing event. For instance, turtles B, D, G and H missed a peak by 2–5 days for their first clutch. During the following inter-nesting interval, they then exhibited a regular first phase (*c.* 14 days) but had a longer (turtles B and D) or a shorter (turtles G and H) second phase before they eventually all nested again during a landing peak (Table 2). This suggests that olive ridley turtles adjust the duration of the second part of their inter-nesting period to synchronize their second clutch with a landing peak. The second half of the inter-nesting interval being thermally independent, it is most likely that behavioural synchronization prior to mass landing is socially mediated through pheromone-like exocrine secretions (Weldon *et al.* 1990). Hormone-mediated induction has

already been described in social animals from invertebrates to mammals (e.g. Berger 1992; Watson *et al.* 2003).

Conclusions

In French Guiana, where the olive ridley population is recovering from the dramatic collapse of the last 2000 years, gravid females present *arribada*-like behaviour, indicating that reproductive synchrony may occur in small populations. This further suggests that in this population, it is possible that the ancestral *arribada* behaviour has not evolved over the short period since the reported population decline, and that the observed increase in the current population has resulted in the maintenance of this species-specific behaviour. One key result of our work is that olive ridleys synchronize their behaviour at sea before mass landing by adjusting the duration of the second half of the inter-nesting interval whilst maintaining the first half of the inter-nesting interval (when *in utero* egg maturation is likely to occur). Further studies are required to assess the actual costs/benefits of adjusting the duration of each phase of the inter-nesting interval in terms of eggs development and fitness.

Despite the striking consistency observed in their at-sea behaviour, the temporal pattern of the landing peaks of olive ridley turtles in French Guiana is not as clear as those known in larger populations. Further research based on long-term monitoring is required to better assess the potential links between population density and proximate cues. This may be achieved by comparing neighbouring populations presenting synchronous/non-synchronous nesting patterns and/or different population trends. Finally, as we have shown that some synchrony occurs in female olive ridleys, a similar approach should focus on reproductive males to better estimate the reproductive/genetic value of such pattern and ultimately the adaptive value of the observed synchronized behaviour.

Table 2. Summary of the nesting events of 10 satellite-tracked olive ridley turtles from French Guiana ($N = 9$) and Suriname ($N = 1^*$)

Turtle's ID	First nest		Second nest	
	Deployment date	No of days before/after a landing peak	Date of the 2nd nesting event	No of days before/after a landing peak
A	30/06/2006 03:33	2/2	27/07/2006 04:03	15/12
B	30/06/2006 08:13	2/2	09/08/2006 03:13	-/1
C	07/07/2006 01:39	5/3	07/08/2006 02:37	26/1
D	07/07/2006 03:35	5/3	08/08/2006 01:05	0
E	20/07/2006 04:00	8/19	21/08/2006 04:00	-/13
F	03/07/2007 05:36	4/3	04/08/2007 04:36	1/4
G	03/07/2007 02:22	4/3	21/07/2007 01:52	0
H	03/07/2007 04:17	4/3	27/07/2007 07:19	0
I*	10/07/2007 05:27	1/7	30/07/2007 06:57	2/4
J	29/06/2007 02:58	0	27/07/2007 03:58	0

The dates of the two nesting events and the time related to an observed landing peak are indicated for each individual (turtles' ID from A to J). '-' means that no landing peak has been identified before the considered nesting event.

In terms of conservation, gathering together in a very restricted coastal area during the last 2 weeks of their interesting interval may expose gravid females to high levels of human activity (e.g. marine navigation, fisheries, pollution) that may jeopardize their survival. As such potential interactions are likely to occur during the critical reproductive period, restoration of the small population of olive ridley turtles in the Guianas will depend on adequate conservation strategies ensuring the efficiency of reproductive activity and survival. The immediate mitigation of threats and the fact that this small population has maintained the ancestral *arribada* reproductive strategy are undeniable key factors for the recovery of this species in the western Atlantic Ocean.

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**Energy expenditure of freely swimming adult green turtles
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RESEARCH ARTICLE

Energy expenditure of freely swimming adult green turtles (*Chelonia mydas*) and its link with body acceleration

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SUMMARY

Marine turtles are globally threatened. Crucial for the conservation of these large ectotherms is a detailed knowledge of their energy relationships, especially their at-sea metabolic rates, which will ultimately define population structure and size. Measuring metabolic rates in free-ranging aquatic animals, however, remains a challenge. Hence, it is not surprising that for most marine turtle species we know little about the energetic requirements of adults at sea. Recently, accelerometry has emerged as a promising tool for estimating activity-specific metabolic rates of animals in the field. Accelerometry allows quantification of the movement of animals (ODBA/PDBA, overall/partial dynamic body acceleration), which, after calibration, might serve as a proxy for metabolic rate. We measured oxygen consumption rates (\dot{V}_{O_2}) of adult green turtles (*Chelonia mydas*; 142.1±26.9 kg) at rest and when swimming within a 13 m-long swim channel, using flow-through respirometry. We investigated the effect of water temperature (T_w) on turtle \dot{V}_{O_2} and tested the hypothesis that turtle body acceleration can be used as a proxy for \dot{V}_{O_2} . Mean mass-specific \dot{V}_{O_2} ($s\dot{V}_{O_2}$) of six turtles when resting at a T_w of 25.8±1.0°C was 0.50±0.09 ml min⁻¹ kg^{-0.83}. $s\dot{V}_{O_2}$ increased significantly with T_w and activity level. Changes in $s\dot{V}_{O_2}$ were paralleled by changes in respiratory frequency (f_R). Deploying bi-axial accelerometers in conjunction with respirometry, we found a significant positive relationship between $s\dot{V}_{O_2}$ and PDBA that was modified by T_w . The resulting predictive equation was highly significant ($r^2=0.83$, $P<0.0001$) and associated error estimates were small (mean algebraic error 3.3%), indicating that body acceleration is a good predictor of \dot{V}_{O_2} in green turtles. Our results suggest that accelerometry is a suitable method to investigate marine turtle energetics at sea.

Key words: sea turtle energetics, accelerometry, diving, oxygen consumption rate, exercise, PDBA, respiratory frequency, body acceleration, resting metabolic rate.

INTRODUCTION

Marine turtles are large ectotherms with a general tropical to subtropical distribution. Six out of seven marine turtle species are currently listed in the International Union for Conservation of Nature (IUCN) red list of threatened species, with a status that ranges from 'vulnerable' to 'critically endangered'. Fundamental for conservation efforts is a clear understanding of marine turtle physiology and ecology. Especially important are the energy relationships of marine turtles; how they acquire and allocate energy. The rate at which organisms take up energy and materials from the environment, transform them, and allocate them to survival, growth and reproduction – in other words, their metabolic rate – controls ecological processes at all levels of organisation: from the fitness of the individual, to population dynamics and ecosystem processes (Brown et al., 2004). Most important for our understanding of the overall energy requirements of marine turtle populations, which will ultimately define population structure and size, is the knowledge of the at-sea metabolic rates of marine turtles (Jones et al., 2004). Measuring the metabolic rates of turtles at sea, however, is not an easy task, given the logistic and methodological constraints. To date, there are only three studies that have investigated the field metabolic rates of marine turtles (Wallace et al., 2005; Clusella Trullas et al., 2006; Southwood et al., 2006) using the doubly labelled water

method (DLW) (Lifson et al., 1955; Speakman, 1997). These studies concerned hatchling olive ridley turtles (*Lepidochelys olivacea*) (Clusella Trullas et al., 2006), juvenile green turtles (*Chelonia mydas*) (Southwood et al., 2006) and adult leatherback turtles (*Dermochelys coriacea*) (Wallace et al., 2005). However, there has been some uncertainty as to whether the DLW method is appropriate to use with marine turtles. The combination of high water turnover rates and low metabolic rates, typically found in marine turtles, might render this method unreliable. A recent validation study with juvenile green turtles that used DLW in combination with respirometry found that the DLW method produced valid results in certain circumstances (fed animals), while it did not in others (fasted animals), and therefore advised a cautionary use with marine reptiles (Jones et al., 2009). Furthermore, the DLW method gives an estimate for the overall energetic costs of an animal during the measurement period, but it does not provide more detailed information (i.e. activity-specific metabolic costs).

Apart from field studies, there have been a considerable number of investigations into the energetics of marine turtles in captive settings during the last decades using respirometry. While these studies have increased our understanding of marine turtle energetics tremendously (Wallace and Jones, 2008), there has been a strong bias towards hatchlings and immature animals. For most species,

we know little about the energy requirements of adult turtles during the different phases of their oceanic life. Furthermore, in respirometry studies, marine turtles have typically been confined to small tanks with little opportunity for swimming, except hatchlings and small juveniles (Wyneken, 1997; Butler et al., 1984). Hence, most of these measurements reflect conditions either during rest (i.e. motionless) or during routine activity (e.g. turtles slowly moving along the tank bottom), while respirometry measurements of actively swimming turtles, apart from hatchlings and small juveniles, are missing.

Recently, a promising new method for estimating activity-specific metabolic rates of animals in the field has been developed. It has become known as 'accelerometry', as it involves the recording of body acceleration of animals (Wilson et al., 2006). Accelerometry is based on the principle that animal movement, realised through muscular contraction, requires energy, so a relationship between movement patterns and energy expenditure can be expected. By attaching accelerometers to animals, we can accurately quantify their overall movement through space over time (referred to as 'ODBA', overall dynamic body acceleration) (*sensu* Wilson et al., 2006) and this might serve as a proxy for energy expenditure. Accelerometry requires calibration with captive animals under controlled conditions, to relate the proxy variable to metabolic rate, which is typically measured as oxygen consumption rate using respirometry. Such calibration studies have been conducted over a range of species, typically involving treadmill exercise and, hence, terrestrial locomotion (Halsey et al., 2009). Interestingly, a significant relationship between body acceleration and metabolic rate was also found during diving in a mammalian diver, the Steller sea lion (*Eumetopias jubatus*) (Fahlman et al., 2008a). Most recently, accelerometry was successfully used with another ectotherm species, the cane toad (*Bufo marinus*) (Halsey and White, 2010). These calibration studies provide predictive equations, allowing estimation of metabolic rate from the recording of body acceleration. The error estimates associated with these predictive equations are generally low, with mean algebraic errors typically $\sim\pm 5\%$ and mean absolute errors $\sim 10\%$ (Halsey et al., 2009). They are therefore similar to the error estimates associated with a more established method that records the heart rate of animals as a proxy of metabolic rate (Butler et al., 2004). However, unlike accelerometry, the heart rate method requires surgical implantation, and while it has been used successfully to investigate the energetics of avian divers over the annual cycle (Green et al., 2009a; White et al., 2011), it has not yet been used to estimate marine turtle energy expenditure. Such investigation might be complicated by the fact that turtles possess a functionally undivided ventricle, so that shunting of blood between the systemic and pulmonary circulation might occur, especially during diving. When diving to depth, the increase in pressure will compress the lungs, so that the functional gas exchange might be altered, further complicating the relationship between heart rate and oxygen consumption. Accelerometry might therefore be the method of choice to investigate marine turtle energetics.

The south-western Indian Ocean hosts important nesting and feeding areas for marine turtles, especially green turtles (e.g. Comoros Islands, Mayotte Island, Scattered Islands) (Bourjea et al., 2007; Lauret-Stepler et al., 2007). For example, at Mayotte Island juvenile and adult green turtles exploit seagrass meadows on a year-round basis (Taquet et al., 2006; Ballorain et al., 2010). Similarly, at Reunion Island foraging juvenile and adult green turtles are present in coral reef zones throughout the year (Jean et al., 2010). Given their year-round presence, turtles are exposed to the seasonal changes in environmental conditions (e.g. water temperature, light

conditions, food availability), which might have profound effects on behavioural patterns and energetics (Southwood et al., 2003; Hochscheid et al., 2004; Ballorain, 2010). Hence, this setting provides a great opportunity to study energy acquisition and allocation of these animals during the different phases of their life cycle in great detail and under natural conditions. A prerequisite for such investigation, however, is to establish a reliable method that can be used to measure the energetic state of turtles in the field.

The aim of our study was (1) to investigate the energy expenditure of adult green turtles during rest and when swimming in a 13-m-long channel; (2) to investigate the effect of seasonal changes in water temperature on turtle energy expenditure; and (3) to test the hypothesis that turtle body acceleration can be used as a proxy for energy expenditure. If verified, the ultimate goal of our study was to establish a predictive equation that could be used to estimate energy expenditure of turtles in the wild from the recording of acceleration.

MATERIALS AND METHODS

Turtles

Six adult female green turtles (*Chelonia mydas* L. 1758) with a body mass (M_b) range of 98.4–170.2 kg and a curved carapace length (CCL) of 103.7 \pm 6.4 cm were used in this study (Table 1). All turtles were captured as hatchlings on Tromelin Island in the Western Indian Ocean (15°53'S, 54°31'E) during the late 1980s. They were raised and maintained at the former Ferme Corail, which is now a public aquarium (Kélonia), Reunion Island (21°06'S, 55°36'E). Turtles were kept communally inside an uncovered concrete pool (13 \times 15 m, 1–2.2 m deep, 300 m³ volume), adjacent to a shallow lagoon, which continuously supplied sea water to the pool at a rate of 150 m³ h⁻¹. Water temperature (T_w) in the turtle pool matched the temperature of the adjacent lagoon and underwent the same seasonal changes (Fig. 1). Given the shallow depth of the adjacent lagoon and the typically strong solar radiation during the day, T_w also underwent considerable daily oscillations, with differences often of ~ 2 – 3°C between day and night. Turtles were exposed to the natural light cycle, with ~ 13.5 h light (10.5 h dark) during the austral summer and ~ 11 h light (13 h dark) during the austral winter. Turtles were fed 5 times a day with a diet consisting of vitamin-supplemented fish pellets (Ecolife 16F N9, BioMar SAS, Nersac, France; ~ 70 g daily) and plant leaves (tree heliotrope, *Heliotropium foertherianum*; ~ 300 g daily). All experimental procedures were approved by the Comité National pour la Protection de la Nature of the French Ministry in charge of Environmental Affairs and adhered to all institutional guidelines and the legal requirements of the country in which the work was carried out.

Experimental set-up

We constructed a swim channel inside the concrete pool where turtles were housed, by subdividing an area (13 m long, 2 m wide) using PVC tubing and plastic fencing (Fig. 2). The depth of the channel was ~ 1 m at one end, from which it sloped gradually to ~ 2.2 m at the opposite end. At the shallow end of the channel a gate was left open, so that turtles could enter and leave the channel of their own volition. Over the course of 3 months the surface of the channel was gradually covered with elements (2 \times 2 m) constructed with PVC tubing and plastic-coated metal fence, securely fastened at a water depth of ~ 10 cm, until only an area of ~ 2 \times 2 m at the shallow end remained open. In parallel with channel construction, we installed an underwater video array that allowed continuous observation of turtles inside the swim channel (Fig. 2). Four black and white video cameras (Model CVC6990, Lorex, MBrands,

Table 1. Oxygen consumption rates and respiratory frequency of adult green turtles when resting and swimming at different water temperatures

Turtle	M_b (kg)	CCL (cm)	T_w (°C)	Resting			Swimming		
				\dot{V}_{O_2} (ml min ⁻¹)	$s\dot{V}_{O_2}$ (ml min ⁻¹ kg ^{-0.83})	f_R (breaths h ⁻¹)	\dot{V}_{O_2} (ml min ⁻¹)	$s\dot{V}_{O_2}$ (ml min ⁻¹ kg ^{-0.83})	f_R (breaths h ⁻¹)
Austral winter									
Elisabeth	120.9±0.3	96	25.8±0.6	21.55±1.33	0.40±0.02	3.7±0.5	43.96±5.52	0.82±0.10	7.8±2.1
Monique	170.2±0.5	108	25.0±0.3	36.17±4.52	0.51±0.06	5.6±0.7	59.80±4.10	0.84±0.06	8.3±1.5
Delphine	156.1±0.4	109	24.5±0.4	32.49±4.63	0.49±0.07	3.7±0.8	50.13±6.63	0.76±0.10	5.2±0.8
Sandy	156.1±1.2	107	25.7±0.9	36.82±7.27	0.56±0.11	6.1±1.9	102.82±13.75	1.55±0.20	18.1±4.4
Nadia	151.0±0.0	107	26.6±0.9	24.96±1.62	0.39±0.03	3.2±0.6	44.32±6.34	0.69±0.10	5.7±0.6
Karima	98.4±1.5	95	27.0±1.0	28.61±3.47	0.63±0.08	5.0±1.0	39.50±4.04	0.88±0.09	5.9±1.1
Grand mean	142.1±26.9	103.7±6.4	25.8±1.0	30.10±6.15	0.50±0.09	4.5±1.2	56.76±23.63 ^b	0.92±0.32 ^b	8.5±4.9 ^b
Austral summer									
Elisabeth	114.7±0.3	96	30.2±0.4	42.62±3.12	0.83±0.06	8.6±1.3	60.30±4.33	1.18±0.09	11.6±1.3
Monique	163.6±1.6	108	29.2±0.9	44.41±4.57	0.65±0.07	7.1±1.6	54.13±5.00	0.79±0.07	7.3±0.9
Delphine	160.2±0.0	109	29.9±0.7	46.61±4.92	0.69±0.07	5.3±1.1	60.96±3.32	0.90±0.05	6.1±0.6
Nadia	148.3±0.7	107	29.2±0.5	33.14±4.19	0.52±0.07	5.0±0.8	48.14±4.34	0.76±0.07	8.5±1.5
Grand mean	146.7±22.3	103.7±6.4	29.6±0.5	41.69±5.93 ^a	0.67±0.13 ^a	6.5±1.7 ^a	55.88±6.01 ^{a,b}	0.91±0.19 ^{a,b}	8.4±2.4 ^{a,b}

Data were obtained during the austral winter (Jun.–Nov. 2009) and austral summer (Jan.–Apr. 2010). Values are means ± s.d. Grand means were established from individual turtle means. Values were averaged from 7–11 trials conducted with each turtle during both seasons. Trial duration was between 3.5 and 4 h, with each trial being split into two periods of contrasting activity status (resting/swimming) based on behavioural observation and acceleration recordings.

Each of these periods per trial, over which mean values were calculated, lasted on average ~1.5 h and consisted of multiple dive cycles (on average ~8 dive cycles, with a minimum and maximum of 3 and 26 dive cycles, respectively).

M_b , body mass; CCL, curved carapace length; T_w , water temperature; \dot{V}_{O_2} , oxygen consumption rate; $s\dot{V}_{O_2}$, mass-specific oxygen consumption rate; f_R , respiratory frequency.

^aSignificant difference from the austral winter; ^bsignificant difference from resting conditions.

Scarborough, ON, Canada) were positioned alongside the channel and connected to a multiplexer (EverFocus Electronics Corp., Taipei, Taiwan) and video monitor inside a small observation hut. This hut was built adjacent to the shallow end of the channel and also housed all respirometry equipment. During these months all turtles entered and left the swim channel on a daily basis and habituated to surface at the increasingly smaller open end of the channel to breathe. Food pellets were used to stimulate turtles to enter the channel and to attract them to the breathing area.

Training and experimental trials

Turtles were weighed before and after participation in each round of experimental trials. To cover the annual range in T_w experienced by wild turtles in this region of the Indian Ocean, we subjected turtles to two rounds of trials. The first round was conducted with six turtles during the austral winter between June and November 2009 (trial T_w : 25.8±1.0°C). This was followed by trials with four of these six turtles during the austral summer between January and April 2010 (trial T_w : 29.6±0.5°C). Body mass changes during each experimental period were negligible (−0.26±2.18% and 0.08±0.89% during austral winter and summer, respectively) but changes between the seasons were larger (−2.04±3.40%, from winter to summer). The experimental period for a turtle was about 4 weeks per season. It started with a training period of 2 weeks, during which each turtle became accustomed to the exact protocol used during the recording period that followed.

Measuring oxygen consumption rates in diving animals requires them to breathe inside a chamber, from which gas samples can be taken. Each turtle therefore had to firstly ‘learn’ the exact position of this chamber, located at the shallow end of the 13 m-long swim channel (Fig. 2), so that she would consistently find it and lift her head into it for breathing. In the morning of a training/recording day a surface area of 2×2 m, at the shallow end of the channel (where

the Plexiglas[®] chamber would eventually be positioned), was still open. A turtle was enclosed inside the swim channel and closely monitored from within the hut. Once inside the swim channel, a turtle typically swam back and forth, interrupted by periods spent resting at the bottom. Over the course of a few hours, the rest of the surface area was gradually covered and the Plexiglas[®] chamber set in place. With increasing cover, a turtle typically became less active and settled at the bottom to rest. Turtles showed a good capacity to ‘learn’ the position of the chamber, so that after a few

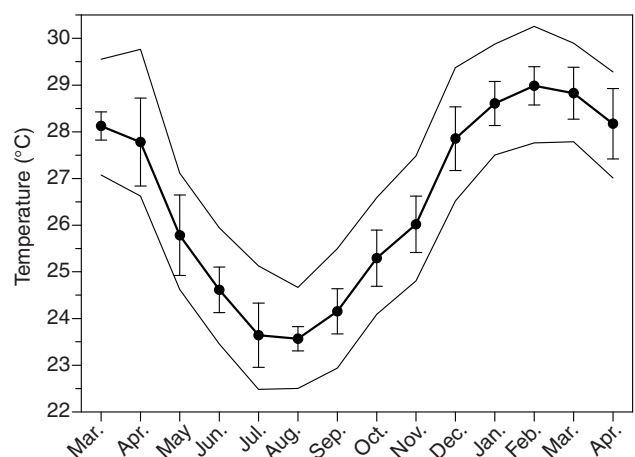


Fig. 1. Seasonal changes in water temperature (T_w , °C) inside the turtle pool between March 2009 and April 2010. The middle line indicates the monthly mean T_w (±s.d.), while the upper and lower lines indicate the mean maximum and minimum temperatures, respectively. Values were calculated from daily means and are based on continuous recordings of a temperature logger.

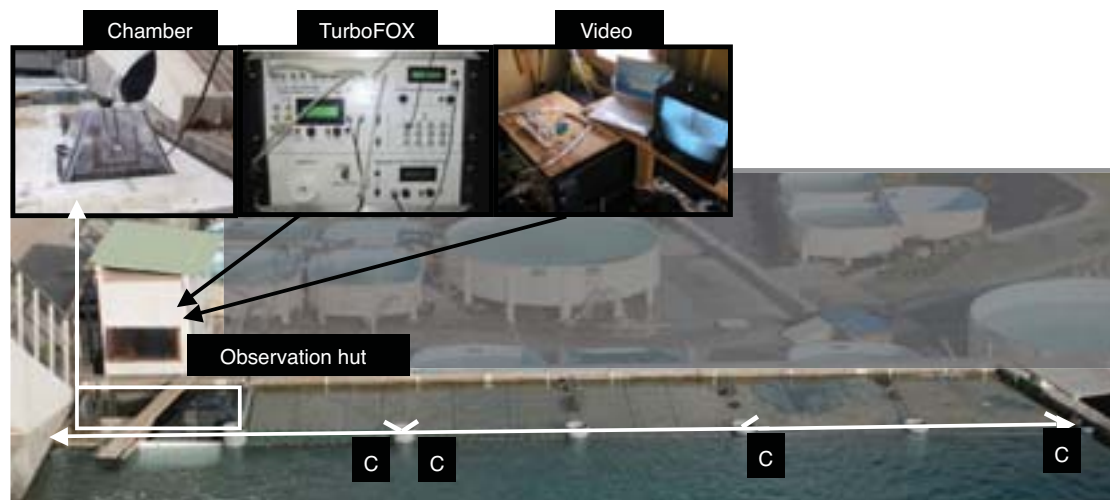


Fig. 2. Experimental set-up, showing the 13-m-long swim channel with a covered surface except in a small area in front of the observation hut (housing respirometry/video equipment and an observer), which was covered with a PVC board during trials, and into which the respirometer chamber was fitted. Positions and orientation of the underwater video cameras (C) are also indicated.

days of training, they all consistently breathed into the chamber without difficulty or apparent excitement. Given the size of our channel, this is remarkable, as the ability of sea turtles to find breathing holes has been questioned for pools of far lesser size (Lutz et al., 1989; Hochscheid et al., 2004).

A recording trial started with a turtle typically settled to rest at the bottom of the channel, just below the chamber. Turtles often rested motionless for long periods (maximum dive duration 44.2 min), only periodically floating upward into the chamber to breathe. Investigating the relationship between oxygen consumption rate (\dot{V}_{O_2}) and body acceleration (partial dynamic body acceleration, PDBA) required the recording of sufficiently long periods with different activity levels (i.e. resting/low activity periods and swim periods; see below). Therefore, if turtles did not start to swim spontaneously after resting for 1.5–2 h, a diver entered the pool (outside the channel) and encouraged the turtle to swim by gently tapping her carapace with a stick. Such motivation was sufficient to initiate swimming. During the swim period the diver swam alongside the turtle (but outside the channel), to closely monitor behaviour and encourage maintained swimming activity. After initial motivation turtles swam completely at their own volition, only occasionally requiring further encouragement.

We made every effort to maintain conditions between trials as stable as possible, especially with respect to T_w , which was monitored continuously using a temperature logger (Minilog-T 8K, Vemco Ltd, Halifax, NS, Canada; submerged at a depth of ~1 m; sampling interval 5 min; resolution 0.1°C; accuracy $\pm 0.5\%$). Given the daily T_w fluctuations, all recordings were conducted during the early afternoon (12–17 h), when T_w conditions were most stable (mean maximum T_w variations during trials $0.5 \pm 0.1^\circ\text{C}$). Recording duration for each trial was between 3.5 and 4 h, split into two periods with contrasting activity levels of similar duration (see below). For each season, 7–11 trials were recorded per turtle. During the experimental period turtles were maintained on their regular feeding regime, so that all turtles participating in trials were in the absorptive state. To ensure a comparable nutritional status for all turtles, food delivery was discontinued 1 h before a trial until its completion.

Respirometry system

Open-circuit respirometry was used to measure \dot{V}_{O_2} of turtles when resting and swimming within the channel. Turtles were trained to breathe within a transparent Plexiglas® chamber in the shape of a truncated pyramid (bottom 38×38 cm, top 19×19 cm, height 24 cm, volume 20 l) with its bottom submerged. Given the forceful exhalation of turtles upon surfacing, their large tidal volume and the relatively small size of our chamber, the chamber was fitted with a latex breathing bag (6.1 l; Deltalyo & Valmy, Roanne, France) to receive overflow expired gas, while a unidirectional breathing valve (Smiths, Rungis, France) was fitted to the inflow opening, ensuring that expired gas would not escape. During exhalation the breathing bag inflated but as soon as exhalation stopped it deflated and its contents were pushed back into the chamber. A small fan inside the chamber provided rapid mixing of expired gas. Air was pulled through the chamber at a rate of 20 l min^{-1} [automatically corrected to standard temperature and pressure (STP), 273 K and 101.3 kPa] and led into the adjacent hut, where it entered the primary flow control unit (FK-100) of a TurboFOX-RM integrated field respirometry system (Sable Systems International, Las Vegas, NV, USA). A subsample (200 ml min^{-1}) was pulled through a humidity meter (RH-300) and scrubbing columns (Drierite, soda lime, Drierite; Xenia, OH, USA) to remove water vapour and CO_2 , before entering the fuel cell oxygen analyser of the TurboFOX-RM unit. Oxygen concentration within the chamber, main flow rate through the chamber, humidity of the gas sample and barometric pressure were recorded every second onto a laptop computer using Expedata (Sable Systems). As all measurements were conducted over seawater, which has a great affinity for CO_2 , we did not measure the latter but scrubbed it from the subsample using soda lime. All connections between the various components of the respirometry system were made using gas-impermeable Bev-a-Line or Tygon tubing. The O_2 analyser was calibrated before each trial using outside air scrubbed of water vapour and CO_2 (set to 20.95% O_2 ; the zero point was fixed and not subjected to drift). The humidity meter was calibrated weekly according to the recommendations of the manufacturer. We used dry 99.995% pure N_2 (Air Liquide, Le Port, Reunion) and a water-saturated air sample to calibrate the water vapour pressure reading (kPa). Before a trial the entire system was tested for leaks by infusing pure N_2 gas. The time delay between an exhalation

into the chamber and a change in oxygen concentration being registered by the gas analyser was ~ 25 s, while it took ~ 4 min for the O_2 signal to return to baseline after a disturbance (i.e. exhalation).

Body acceleration

In parallel with respirometry, we deployed a bi-axial acceleration data logger (M190L-D2GT; length 53 mm, diameter 15 mm, mass 17 g; 12-bit resolution; recording range ± 3 g; Little Leonardo, Tokyo, Japan) to record body acceleration of turtles. The logger was set to record heave and surge at a frequency of 16 Hz. Before deployment, the logger was fitted snugly into a custom-made base (made from rubber and lined with Velcro™). A Velcro patch was glued to the centre of the second vertebral scute of a turtle in anterior–posterior direction, before a series of trials started. This allowed for an easy attachment of the streamlined logger base to a turtle before a trial and for its quick removal afterwards, while the turtle remained inside the water channel. Care was taken to attach the logger in the same position during all trials. After a trial, data from the logger were downloaded onto a PC.

Data analysis

Respirometry data were analysed using Expedata. During analysis, O_2 analyser drift and lag time of the respirometry system were corrected for. Main flow rate was corrected to STP dry (STPD) using equation 8.6 in Lighton (Lighton, 2008):

$$FR_c = FR (BP - WVP) / BP, \quad (1)$$

where FR_c is the dry-corrected flow rate, FR is the uncorrected flow rate, BP is the barometric pressure (kPa) and WVP is the water vapour pressure (kPa). \dot{V}_{O_2} was calculated using equation 4b in Withers (Withers, 1977), which is nearly independent of the respiratory quotient (RQ):

$$\dot{V}_{O_2} = FR_e (F_{I_{O_2}} - F''_{E_{O_2}}) / [1 - F_{I_{O_2}} + RQ (F_{I_{O_2}} - F''_{E_{O_2}})], \quad (2)$$

where FR_e is the excurrent flow rate, $F_{I_{O_2}}$ is the fractional concentration of the incurrent O_2 , and $F''_{E_{O_2}}$ is the fractional concentration of the excurrent O_2 (scrubbed of water vapour and CO_2). We assumed a RQ of 0.85.

Our analysis of turtle \dot{V}_{O_2} was based on multiple dive cycles and considered entire periods with contrasting activity levels (see below). We chose this approach despite the fact that the dive duration of turtles was typically sufficiently long (i.e. >5 min) and our respirometry system sufficiently fast to allow calculation of \dot{V}_{O_2} on the level of single dive cycles. The rationale behind this was that preliminary analysis of \dot{V}_{O_2} during resting trials returned highly variable values when calculated on the basis of single dive cycles, suggesting that turtles might not have reloaded their oxygen stores to identical levels during each surface interval. Consequently, oxygen uptake (V_{O_2}) after a dive might not necessarily reflect oxygen consumption rate (\dot{V}_{O_2}) during that particular dive. During these trials, turtles exhibited a wide range of dive durations but typically only took a single breath between dives. While there was a significant increase in oxygen uptake after a dive as dive duration increased (Fig. 3A), this increase was so small, considering the range of dive durations, that reloading of the oxygen stores to identical levels between dives could not have occurred. Consequently, \dot{V}_{O_2} would be underestimated during long dives and overestimated during short dives. A plot of dive duration *versus* \dot{V}_{O_2} suggested that \dot{V}_{O_2} during short dives (5 min) was 4–5 times higher than during long dives (20 min), while turtles rested motionless at the bottom in both cases (Fig. 3B). By contrast, oxygen uptake after a 20 min dive was only $\sim 40\%$ greater than after a 5 min dive. We are therefore convinced that the large differences in \dot{V}_{O_2} we observed

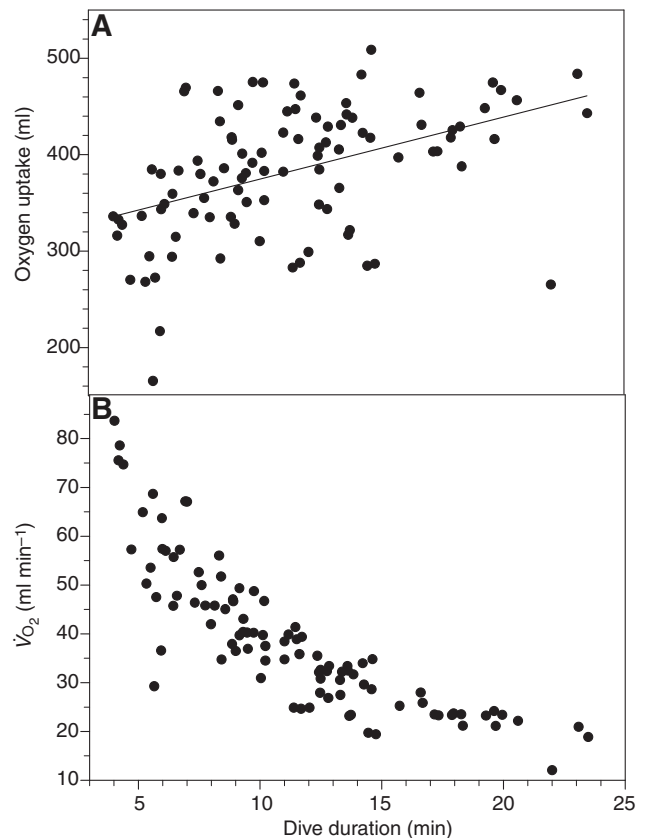


Fig. 3. (A) Oxygen uptake (V_{O_2}) after resting dives and (B) oxygen consumption rate (\dot{V}_{O_2}) during these dives against dive duration for one turtle [Elisabeth, body mass (M_b) 117.7 kg, T_w 29.9 \pm 0.9°C, 97 dives during 8 trials; single dive cycle resolution]. While there was a significant increase in V_{O_2} after a dive with increasing dive duration ($y=6.42x+310.25$; $r^2=0.19$, $F=23.78$, $P<0.0001$), this increase was so small, considering the range of dive durations, that reloading of the oxygen store to identical levels between dives could not have occurred. Hence, the fourfold to fivefold difference in \dot{V}_{O_2} between long and short dives (B) is an artefact, related to the breathing pattern displayed by our turtles (single breaths), habituated to dive in a shallow pool. Consequently, the \dot{V}_{O_2} values plotted here do not reflect the true energetic costs of these dives and we therefore based our analysis on multiple dive cycles (see Materials and methods).

between short and long resting dives are an artefact related to the particular breathing pattern displayed by our turtles (single breaths), habituated to dive in a shallow pool. Interestingly, incomplete reloading of the oxygen store during brief periods at the surface has also been observed in mammalian divers. For example, during foraging dives conducted in quick succession, Steller sea lions ran down their oxygen store, which was only completely reloaded during longer surface intervals (Fahlman et al., 2008b). Highly variable oxygen consumption rates were also observed in juvenile and adult loggerhead turtles (*Caretta caretta*) diving in a small/shallow tank, when \dot{V}_{O_2} was calculated over single dive cycles (Hochscheid, 2003). Consequently, if oxygen reloading is incomplete during single dive cycles in our turtles, calculation of \dot{V}_{O_2} requires consideration of multiple dive cycles, when this is more likely to be achieved.

Each trial was split into two periods of contrasting activity level based on behavioural observations and acceleration recordings: a resting/low activity period and a swim period (Fig. 4). Experimental design and turtle behaviour allowed us to clearly separate these

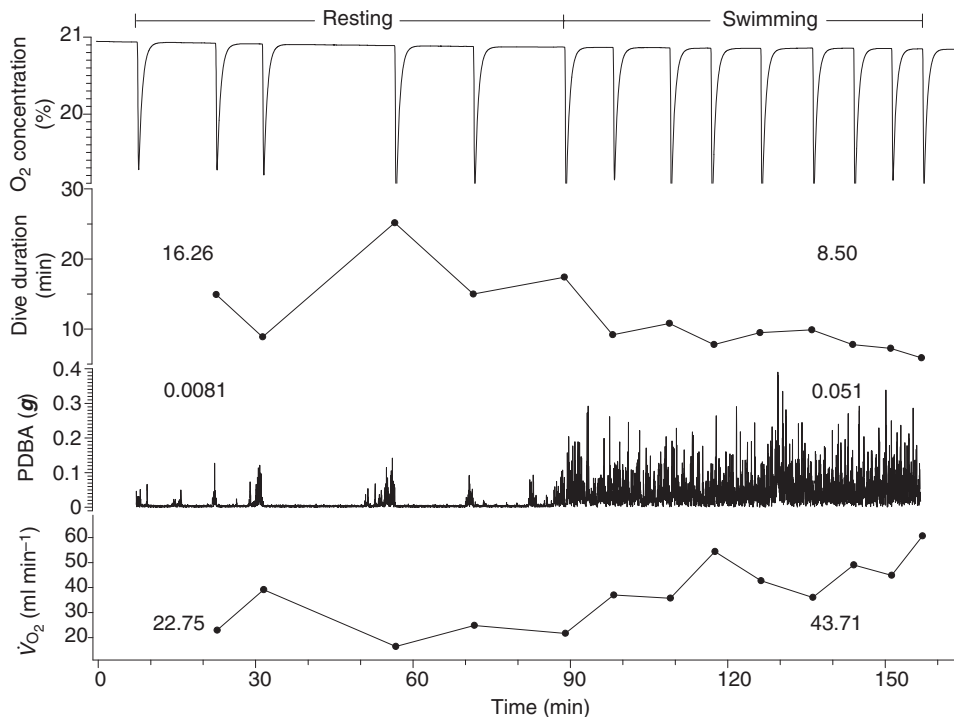


Fig. 4. Example of combined respirometry and accelerometry recording during a typical trial with one turtle. Traces (from top to bottom) show the O_2 concentration inside the chamber, dive duration, partial dynamic body acceleration (PDBA) and \dot{V}_{O_2} . The downward deflections in the top trace reflect breathing events. Dive duration was calculated as the time elapsed between two consecutive breathing events. PDBA was calculated from turtle body acceleration (surge and heave), recorded in parallel with respirometry using a bi-axial acceleration logger. \dot{V}_{O_2} for single dive cycles was calculated from the area under the curve associated with each breathing event in a continuous plot of apparent \dot{V}_{O_2} against time. However, in our analysis, we did not use a single dive cycle resolution but divided each trial into two periods with contrasting activity level (indicated by the bars at the top) and calculated \dot{V}_{O_2} over these periods. For each trace two numbers are given, representing the calculated values for the resting and swimming period of that particular trial, included in the analysis.

periods. If brief periods of mixed activity occurred during a trial (i.e. a turtle alternated resting and swimming), they were excluded from further analysis. Periods from each trial included in the analysis were of similar duration (~ 1.5 h on average) and were used to calculate \dot{V}_{O_2} (ml min^{-1}), PDBA (g) and respiratory frequency (f_R , breaths h^{-1}) (Fig. 4). \dot{V}_{O_2} was calculated as the total oxygen uptake during a period divided by period duration. To account for the variation in \dot{V}_{O_2} between individuals associated with differences in M_b , we also report \dot{V}_{O_2} mass independently as $s\dot{V}_{O_2}$ ($\text{ml min}^{-1} \text{kg}^{-0.83}$). The scaling exponent of 0.83 has commonly been used in the turtle literature (Prange and Jackson, 1976; Southwood et al., 2003) and is similar to the exponent we found during separate resting trials with nine turtles (0.87; M_b range 9.7–166.2 kg; mean T_w $29.2 \pm 1.4^\circ\text{C}$; M.R.E., S.C. and J.-Y.G., unpublished). f_R was determined as the number of breaths divided by the length of the measurement period.

From the recorded acceleration data (surge and heave) we calculated a trace of PDBA for each trial following Wilson and colleagues (Wilson et al., 2006). Briefly, recorded data from both axes were first converted into absolute acceleration values (g) using our calibration equations. We removed the static/low frequency component of acceleration (due to animal posture) by smoothing each axis using running means over 4 s, based on observed flipper beat cycle durations (Fig. 5) (Shepard et al., 2008), which were then subtracted from the unsmoothed data of both axes, to produce an approximation of dynamic acceleration (high frequency component; due to the active movement of the animal). After converting these derived values into absolute positive units, values from both axes were summed to produce a trace of PDBA. Logger and respirometry time were synchronised and mean values of PDBA were calculated for the periods identified as 'resting/low activity' and 'swimming' for all trials. Each period consisted of multiple dive cycles (on average ~ 8 dive cycles for both activity levels, with a minimum and maximum of 3 and 26 dive cycles, respectively).

Statistical analysis

All statistical analyses were conducted using JMP (v.8.0.2.2, SAS Institute Inc., Cary, NC, USA). Differences in oxygen consumption rates (\dot{V}_{O_2} and $s\dot{V}_{O_2}$) and respiratory frequency (f_R) during different activity states (resting *versus* swimming) and during different seasons (austral winter *versus* summer) were tested using a linear mixed-effects model (standard least-squares regression fitted by REML) (Table 1). Activity status and season were included as fixed effects, while turtle ID was included as a random effect. A linear mixed-effects model (LME) was also used to investigate the relationship between $s\dot{V}_{O_2}$ and PDBA during diving. Because our goal was to produce a predictive equation for $s\dot{V}_{O_2}$ that could be used to investigate the energetics of green turtles in the wild and as T_w strongly affects turtle $s\dot{V}_{O_2}$, we also included T_w in the model. Hence, we included PDBA and T_w as fixed effects, while turtle ID was included as a random effect. We further tested whether the relationship between $s\dot{V}_{O_2}$ and PDBA varied with activity status (PDBA \times activity status) and between individuals (PDBA \times turtle ID). Finally, we ran the model without the interaction terms to produce a common predictive equation for $s\dot{V}_{O_2}$ based on PDBA and T_w .

We used a jack-knife procedure to validate the common predictive equation calculating $s\dot{V}_{O_2}$ from PDBA and T_w (Sokal and Rohlf, 1981; Halsey and White, 2010). Data for one individual were removed from the data set and a new predictive equation was calculated from the remaining data set. PDBA and T_w recorded during trials of the excluded individual were fed into the new predictive equation to estimate its $s\dot{V}_{O_2}$. These $s\dot{V}_{O_2}$ estimates were compared with the $s\dot{V}_{O_2}$ values measured concurrently with PDBA and T_w for that individual. This procedure was conducted sequentially for all individuals and mean algebraic error, mean absolute error and the range of errors for individuals were computed as percentage errors [(estimated value – observed value) $\times 100$ /observed value].

Significance for all statistical tests was accepted at $P < 0.05$. All mean values are presented ± 1 s.d.

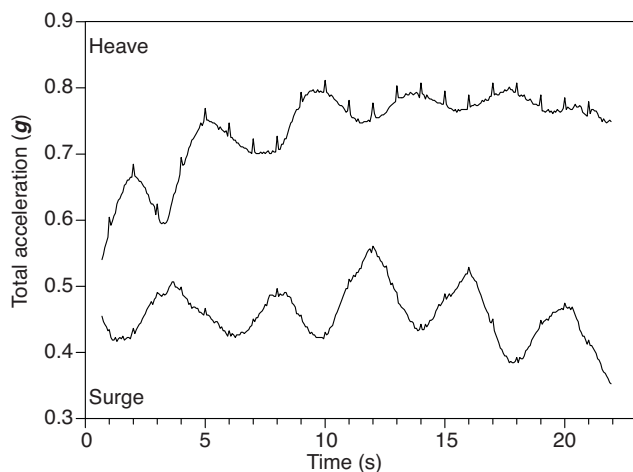


Fig. 5. Typical acceleration trace recorded from one turtle swimming in the channel. Shown is the total acceleration in the dorso-ventral direction (heave, top) and in antero-posterior direction (surge, bottom). Individual cycles, visible especially in the surge trace, correspond to flipper beat cycles.

RESULTS

\dot{V}_{O_2} , $s\dot{V}_{O_2}$ and f_R during resting and swimming and the effect of T_w

Mean \dot{V}_{O_2} of resting turtles during the austral winter (mean T_w $25.8 \pm 1.0^\circ\text{C}$) was $30.10 \pm 6.15 \text{ ml min}^{-1}$, corresponding to $0.50 \pm 0.09 \text{ ml min}^{-1} \text{ kg}^{-0.83}$ (Table 1). LME model analysis revealed that both water temperature (for \dot{V}_{O_2} : $F=21.27$, $P<0.0001$; for $s\dot{V}_{O_2}$: $F=28.87$, $P<0.0001$) and activity level (for \dot{V}_{O_2} : $F=194.92$, $P<0.0001$; for $s\dot{V}_{O_2}$: $F=204.02$, $P<0.0001$) significantly affected oxygen consumption rates (Table 1). A mean increase in T_w of $4.1 \pm 1.2^\circ\text{C}$ during the austral summer over winter conditions resulted in a mean increase in $s\dot{V}_{O_2}$ during rest of $52.2 \pm 36.6\%$ ($N=4$). Similarly, $s\dot{V}_{O_2}$ during swimming was increased on average by $86.4 \pm 50.5\%$ during winter and by $34.8 \pm 10.7\%$ during summer, when compared with resting dives. f_R of resting turtles during the austral winter was $4.54 \pm 1.19 \text{ breaths h}^{-1}$ and increased significantly with an increase in T_w ($F=17.17$, $P<0.0001$) and activity level ($F=77.51$, $P<0.0001$; Table 1). We found a significant linear relationship between f_R and $s\dot{V}_{O_2}$ (Fig. 6; $F=727.19$, $P<0.0001$, $r^2=0.88$), the slope of which was not affected by activity level ($P=0.44$) or T_w ($P=0.76$). Breathing patterns in both resting and swimming turtles typically consisted of single breaths during the short surface periods between dives. Only occasionally would turtles take multiple breaths during a surface period and this usually occurred after long dives.

Using body acceleration to estimate \dot{V}_{O_2} during diving

Activity levels during the swim periods differed between trials and between turtles, resulting in a wide range of \dot{V}_{O_2} and PDBA values (Fig. 7) for these periods. The LME model indicated a significant relationship between $s\dot{V}_{O_2}$ and PDBA ($P<0.0001$) as well as T_w ($P<0.0001$). There was no interaction between PDBA and activity status (resting versus swimming; $P=0.69$), indicating that the relationship between $s\dot{V}_{O_2}$ and PDBA did not vary with activity status. However, the slope of the relationship between $s\dot{V}_{O_2}$ and PDBA varied between individuals, as indicated by the significant interaction between PDBA and turtle ID ($P<0.0001$). After removing the interaction terms,

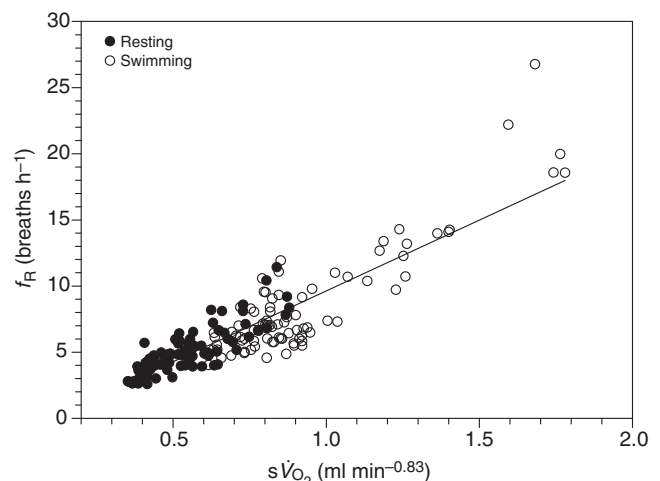


Fig. 6. Relationship between respiratory frequency (f_R) and mass-specific oxygen consumption ($s\dot{V}_{O_2}$) during resting (filled circles) and swimming (open circles) in six adult green turtles ($n=165$ observations). Linear mixed-effects (LME) analysis revealed that the slope of the relationship was not affected by activity level ($P=0.44$) or T_w ($P=0.76$). The solid line indicates the common relationship, established from LME analysis and is best described by: $y=10.712x-1.084$; $F=727.19$, $P<0.0001$, $r^2=0.88$.

the same model ($s\dot{V}_{O_2} = \text{PDBA} + T_w + \text{turtle ID} [\text{random}]$) was used to generate a common predictive equation, which is given by:

$$s\dot{V}_{O_2} = 12.17 \text{PDBA} + 0.03 T_w - 0.46, \quad (3)$$

where $s\dot{V}_{O_2}$ is in $\text{ml min}^{-1} \text{ kg}^{-0.83}$, PDBA is in g and T_w is in $^\circ\text{C}$ ($r^2=0.83$, $N=6$ turtles, $n=170$ observations during 89 trials; for PDBA: $F=519.57$, $P<0.0001$; for T_w : $F=48.98$, $P<0.0001$). The relationship between $s\dot{V}_{O_2}$ and PDBA for six adult green turtles over a range of activity levels is illustrated in Fig. 7. For the purpose of this plot, $s\dot{V}_{O_2}$ values were adjusted to the mean T_w during trials ($27.2 \pm 2.1^\circ\text{C}$, range $23.9\text{--}31.3^\circ\text{C}$), using Q_{10} values established for each individual in separate resting trials (T_w range $22.0\text{--}32.1^\circ\text{C}$) (M.R.E., S.C. and J.-Y.G., unpublished). The validation exercise (Table 2) returned a mean algebraic error of 3.3% (range: -20.0% to 22.9%) and a mean absolute error of 17.1% (range 7.9% to 23.0%).

DISCUSSION

This is, to the best of our knowledge, the first study using respirometry (1) to investigate the energetic costs associated with diving in resting and actively swimming adult sea turtles, and (2) to assess the suitability of the accelerometry method to study sea turtle energetics. Resting metabolic rates of our adult green turtles during submergence were low when compared with literature values concerning adult green turtles resting on the beach and juveniles routinely active in small tanks (see below). The scope of the increase in metabolic rate over the resting rate that we observed during swimming was relatively small (Table 1), underlining the cost efficiency of underwater locomotion in marine turtles, when compared with terrestrial locomotion. Water temperature significantly affected the metabolic rate of turtles during resting dives and when swimming (Table 1). We found a tight relationship between body acceleration (PDBA) of green turtles and associated oxygen consumption rates ($s\dot{V}_{O_2}$) during diving (Fig. 7), indicating that PDBA might serve as a reliable proxy of turtle metabolic rate. The resulting predictive equation is a starting point in our endeavour to investigate the energetic requirements of adult green turtles in the wild.

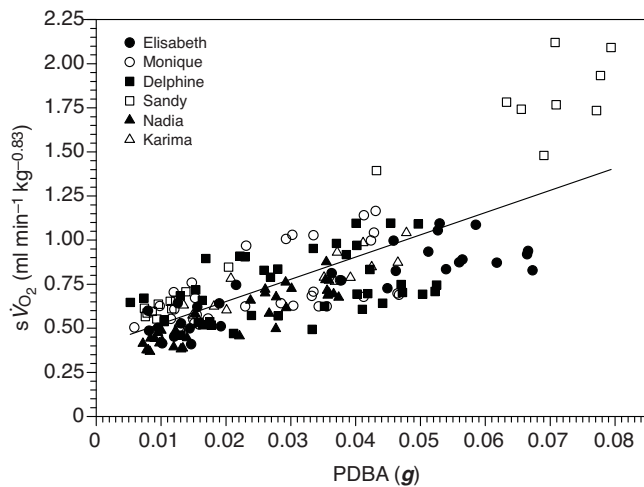


Fig. 7. Rate of $s\dot{V}_{O_2}$ versus PDBA for six adult green turtles over a range of activity levels ($n=170$ observations during 89 trials). For the purpose of this plot, $s\dot{V}_{O_2}$ values were adjusted to the mean T_w during trials ($27.2 \pm 2.1^\circ\text{C}$, range $23.9\text{--}31.3^\circ\text{C}$), using Q_{10} values established for each individual in separate resting trials (T_w range $22.0\text{--}32.1^\circ\text{C}$). The line indicates the common relationship, established from a LME model and is best described by $y=12.61x+0.40$ ($r^2=0.75$, $F=313.51$, $P<0.0001$).

Resting metabolism

Metabolic rate measurements for adult green turtles during submergence do not exist in the literature. The only measurements concerning adult green turtles (mean M_b 128 kg) available in the literature were realised with females after completion of nesting activity (Prange and Jackson, 1976; Jackson and Prange, 1979). In these studies, average metabolic rate of four nesting females resting on the beach (air temperature, T_a $23\text{--}27^\circ\text{C}$) was reported as $0.93\text{ ml min}^{-1}\text{ kg}^{-0.83}$. A further five females were captured and moved to the laboratory, where their oxygen consumption when resting in air (T_a $26\text{--}30^\circ\text{C}$) was considerably higher ($2.28\text{ ml min}^{-1}\text{ kg}^{-0.83}$) and increased about fourfold during exercise in air to $8.79\text{ ml min}^{-1}\text{ kg}^{-0.83}$ (Jackson and Prange, 1979). While not elaborating on this substantial difference between resting measurements, the authors suggested that the lower value measured on the beach probably approximates the ‘true standard metabolism for nesting turtles’. The $s\dot{V}_{O_2}$ we measured during resting dives in our turtles (0.50 and $0.67\text{ ml min}^{-1}\text{ kg}^{-0.83}$ during the austral winter and summer, respectively; Table 1) is below this suggested standard

metabolic rate. However, our turtles were non-reproductive, so differences in the physiological state of these two groups of turtles might explain the difference in metabolic rate. Certainly, reproduction is a physiologically demanding time for turtles (migration, mating, nesting), where hormonal status will be altered (Hamann et al., 2003), with potential consequences for overall metabolism. In addition, being on land, without the structural support provided by seawater, might be physically challenging for sea turtles. Consequently, \dot{V}_{O_2} levels from nesting turtles (in air) may not be good approximations of \dot{V}_{O_2} for turtles in water.

Our resting measurements are also lower than values reported for juvenile green turtles. In a seasonal acclimation study, $s\dot{V}_{O_2}$ of fasting and routinely active juvenile green turtles (mean M_b $24.1\text{--}32.5\text{ kg}$) ranged between $0.58\text{ ml min}^{-1}\text{ kg}^{-0.83}$ in winter (T_w 17°C) and $0.89\text{ ml min}^{-1}\text{ kg}^{-0.83}$ in summer (T_w 26°C) (Southwood et al., 2003). Similarly, Jones and colleagues reported values of 0.80 and $1.63\text{ ml min}^{-1}\text{ kg}^{-0.83}$ for routinely active juvenile green turtles when fasted and fed, respectively (mean M_b $22.0\text{--}22.4\text{ kg}$; T_w $25.1\text{--}25.8^\circ\text{C}$) (Jones et al., 2009). While part of the difference between our measurements on adults and these studies on juvenile turtles may be related to the different life history stages, most may be explained by the different activity levels of turtles. During our resting measurements turtles generally rested motionless at the bottom of the swim channel, only periodically floating up to exchange gases within the chamber, before sinking again to the bottom. By contrast, in previous studies juvenile turtles were routinely active, either resting at the bottom of a small tank or slowly paddling/shuffling along (Southwood et al., 2003; Jones et al., 2009). Figure 2 in Southwood et al. (Southwood et al., 2003) clearly illustrates the effect of activity on turtle $s\dot{V}_{O_2}$, where $s\dot{V}_{O_2}$ increases significantly with activity level. It also shows that $s\dot{V}_{O_2}$ values reported for juvenile turtles in that study corresponded to activity levels of $\sim 40\%$ (i.e. turtles were active for $\sim 40\%$ of a trial). Only during winter conditions did turtles reduce their activity level to below 20% , with correspondingly lower $s\dot{V}_{O_2}$ values (Southwood et al., 2003). Nevertheless, the metabolic rates of our resting turtles remain low in comparison, as our turtles continued feeding between daily trials (absorptive), while the metabolic rates reported for juveniles mostly concern unfed turtles.

In the absence of diving metabolic rate measurements on adult green turtles, Hays and colleagues (Hays et al., 2000) constructed a bioenergetics model to estimate turtle oxygen stores and oxygen consumption during resting dives. Their model was based on time–depth data recorded from green turtles during the interesting period at Ascension Island (Atlantic Ocean) and literature values concerning oxygen storage capacity. It was also assumed that turtles

Table 2. Results of validation exercise

Turtle	Observed $s\dot{V}_{O_2}$ ($\text{ml min}^{-1}\text{ kg}^{-0.83}$)	Estimated $s\dot{V}_{O_2}$ ($\text{ml min}^{-1}\text{ kg}^{-0.83}$)	Estimated–observed $s\dot{V}_{O_2}$ ($\text{ml min}^{-1}\text{ kg}^{-0.83}$)	Algebraic error (%)	Absolute error (%)
Elisabeth	0.84	0.86	0.02	6.9	22.0
Monique	0.70	0.72	0.01	2.0	12.0
Delphine	0.71	0.76	0.05	5.5	17.5
Sandy	1.00	0.74	−0.26	−20.0	20.0
Nadia	0.59	0.70	0.11	22.9	23.0
Karima	0.76	0.77	0.02	2.5	7.9
Grand mean	0.77 ± 0.14	0.76 ± 0.06	-0.01 ± 0.13	3.3	17.1

Shown are the observed and estimated mass-specific oxygen consumption rates ($s\dot{V}_{O_2}$) of adult green turtles during diving and associated error estimates (see Materials and methods for details).

Values are means calculated from 170 observations during 89 trials (7–20 trials per turtle).

A grand mean (\pm s.d.) is the mean of the individual turtle means.

The mean algebraic error takes the difference of the sign into account, while the mean absolute error does not.

would alter lung inflation to control their buoyancy so as to be slightly negative at resting depth. They estimated the $s\dot{V}_{O_2}$ during resting dives for two green turtles with a M_b of 150.6 and 236.5 kg to be 0.63 and $0.84 \text{ ml min}^{-1} \text{ kg}^{-0.83}$, respectively. While their estimates rest on a great number of assumptions (most importantly, the depth at which negative buoyancy is reached with fully inflated lungs), they are similar to the values measured in our turtles during the austral summer (Table 1). Hays and colleagues did not report T_w in their study (Hays et al., 2000) but given it was carried out during the austral summer, T_w was presumably within a similar range to that of our study.

Effect of activity on metabolism

During swimming, $s\dot{V}_{O_2}$ of turtles was significantly elevated when compared with resting. The mean factorial increase in $s\dot{V}_{O_2}$ during swimming was 1.9 (maximum 3.5) in the austral winter and 1.3 (maximum 1.7) in the austral summer. While these values are certainly much lower than those reported from nesting green turtles crawling on the beach (8.9 times resting) (Prange and Jackson, 1976), they are similar to values obtained from juvenile green turtles during swimming (Prange, 1976; Butler et al., 1984). Prange reported an increase in oxygen consumption of 1.6–3.3 times the resting values in juvenile turtles swimming at a speed of between 0.14 and 0.35 m s^{-1} (Prange, 1976). Similarly, Butler and colleagues observed an increase of 1.9–2.8 times resting oxygen consumption in juvenile turtles swimming at a speed of between 0.4 and 0.6 m s^{-1} (Butler et al., 1984). We did not determine the swim speed of our turtles systematically but turtles generally swam at a low pace, rarely exceeding 0.3 m s^{-1} . As they were not swimming in a flume but in a still-water channel, they did not maintain a constant speed throughout. They also had to turn at the end of the channel and frequently engaged in other activities, like investigating the channel bottom. It is therefore not surprising that, on average, we observed a relatively low factorial increase in $s\dot{V}_{O_2}$ during swimming. However, at times turtles swam at an increased speed (albeit for short periods) and in these cases $s\dot{V}_{O_2}$ was increased to a much greater degree, as indicated by the observed maximum factorial increase of 3.5 times resting. Certainly, adult green turtles might be able to increase $s\dot{V}_{O_2}$ during swimming to a much greater degree than what we typically observed within our set-up. Nevertheless, our results demonstrate that swimming in marine turtles is far less demanding than terrestrial locomotion (Prange and Jackson, 1976). This is underlined by the relatively low field metabolic rate (FMR) values found in interesting leatherback turtles ($35 \text{ kJ kg}^{-1} \text{ day}^{-1}$) (Wallace et al., 2005). By contrast, FMR values of juvenile green turtles foraging in Australia were found to be relatively high (142 and $81 \text{ kJ kg}^{-1} \text{ day}^{-1}$ during summer and winter, respectively) (Southwood et al., 2006). The difference between the FMR values of adult leatherback and juvenile green turtles might, at least partially, be explained by the great size difference between species and differences in feeding status during investigation. Nevertheless, the FMR values for juvenile green turtles in Australia are 8.5 to 10 times the metabolic rates of routinely active juvenile green turtles of slightly greater mass in captivity, reported by the same authors (Southwood et al., 2003). While it is not surprising to find higher metabolic rates in the field than in the laboratory, as activity levels might be greater in the field, the amplitude of this difference is remarkable. However, differences in the feeding status of turtles in the studies concerned might again be responsible for some of this, while methodological uncertainties with the derivation of metabolic rates from DLW studies might have led to an overestimation of turtle FMR values. In their validation study, Jones and colleagues argued that a different equation should be applied to determine the

metabolic rates of marine turtles from DLW studies (Jones et al., 2009). Doing so would lower the above FMR values of foraging juvenile green turtles by 37% (Jones et al., 2009).

Effect of temperature on metabolism

$s\dot{V}_{O_2}$ of turtles was significantly affected by T_w (Table 1). In the four turtles measured during both seasons, a mean temperature increase of 4.1°C between the austral winter and summer resulted in an average increase in resting $s\dot{V}_{O_2}$ of 52%. Clearly, temperature strongly influences biochemical reaction rates and, hence, physiological processes. The effect of temperature on ectotherm metabolism, including sea turtles, has been documented in the literature. Early investigators found that oxygen consumption rates of juvenile green turtles in the laboratory, exposed to acute temperature changes between 15 and 35°C , changed fourfold to fivefold (Kraus and Jackson, 1980; Davenport et al., 1982). A similar thermal dependence of metabolism was also reported for juvenile and adult loggerhead turtles during both acute (Lutz et al., 1989) and seasonal temperature changes (Hochscheid et al., 2004). In a recent study on juvenile green turtles, Southwood and colleagues simulated seasonal changes and, when accounting for feeding and activity status, found a rather moderate decrease in their metabolism (24–27%) when temperature declined from 26 to 17°C (Southwood et al., 2003). They concluded that the thermal dependence of green turtle metabolism might be relatively low over the temperature range they naturally encounter. Nevertheless, FMR of juvenile green turtles foraging on the Great Barrier Reef was shown to be considerably increased (75%) during summer ($T_w 25.8^\circ\text{C}$) when compared with the winter ($T_w 21.4^\circ\text{C}$) (Southwood et al., 2006). Some of this difference, of course, might be explained by different activity levels and feeding status during the two seasons. The temperature effect on metabolism of our turtles was less pronounced during swimming (Table 1). The $s\dot{V}_{O_2}$ of four turtles swimming during winter and summer changed on average by 17%. While this could be related to a difference in exercise intensity between seasons, we did not find evidence for this, as mean PDBA of turtles (indicating swimming effort) was similar during the two seasons.

Respiratory frequency (f_R)

Our turtles displayed a breathing pattern that typically consisted of single breaths during the short surface intervals between dives, regardless of activity status. Such a pattern has been observed in other captive marine turtles, typically confined to shallow tanks. For example, Lutz and Bentley found that single breaths were the norm in juvenile green and loggerhead turtles, and observed multiple breaths only occasionally after long dives (Lutz and Bentley, 1985). By contrast, Lutcavage and Lutz reported breathing episodes in immature loggerhead turtles that consisted mostly of two breaths and observed an increase in the number of breaths per episode with dive duration (Lutcavage and Lutz, 1991). An increase in the number of breaths per episode with dive duration was also observed in captive juvenile and adult hawksbill turtles (*Eretmochelys imbricata*) (M.R.E., S.C. and J.-Y.G., unpublished). Within our set-up, green turtles would only occasionally take multiple breaths, typically after long resting dives. However, when diving to depth, green turtles around Reunion Island and Mayotte Island are frequently seen to take multiple breaths at the surface before descending again (M.R.E., unpublished; K. Ballorain unpublished). Hence, the single breath pattern observed in captive turtles might be related to the shallow depth of their holding facilities, where air can be accessed easily, often by simply lifting the head. Mean f_R of our turtles during rest (4.5 – $6.5 \text{ breaths h}^{-1}$; Table 1) and when swimming ($8.5 \text{ breaths h}^{-1}$) was lower than f_R reported for routinely active juvenile green turtles (9.1 and $12.3 \text{ breaths h}^{-1}$ for

winter and summer, respectively) (Southwood et al., 2003), which might be related to the size difference of turtles in the two studies. In our study, f_R increased significantly with increases in T_w and activity level (Table 1). A number of marine turtle studies have found a marked change in f_R with T_w and activity level (Prange and Jackson, 1976; Jackson and Prange, 1979; Butler et al., 1984; Hochscheid et al., 2004). In most marine turtles, such an increase in f_R seems to be the major mechanism to increase ventilation that parallels the increase in \dot{V}_{O_2} , while tidal volume changes little (Prange and Jackson, 1976; Jackson and Prange, 1979; Luttcavage and Lutz, 1997). The significant relationship between f_R and $s\dot{V}_{O_2}$ during resting and swimming that we found (Fig. 6) indicates that this is also the case in adult green turtles.

Using PDBA to estimate $s\dot{V}_{O_2}$ during diving

We found a highly significant positive relationship between PDBA and $s\dot{V}_{O_2}$ in our turtles during diving that was modulated by T_w (Fig. 7), suggesting that body acceleration of turtles might serve as a good proxy of energy expenditure during diving. From this it was possible to generate a significant predictive equation (Eqn 3) that allows estimation of turtle $s\dot{V}_{O_2}$ from the recording of PDBA and T_w . A validation exercise returned mean algebraic and absolute errors that are small (Table 2) and similar to those of other studies deploying both the accelerometry and the heart rate method to estimate the energy expenditure of animals (Halsey et al., 2009). This makes accelerometry a promising tool to investigate the at-sea metabolic rates of marine turtles.

Since its first application to animal biology (Wilson et al., 2006), the accelerometry method has been deployed in a wide range of species and its validity to estimate energy expenditure has been assessed (Halsey et al., 2009; Green et al., 2009b). While most studies originally centred on terrestrial locomotion in mostly endotherm species, there are now a number of studies on semi-aquatic/aquatic species and ectotherms (Halsey et al., 2011; Fahlman et al., 2008a; Payne et al., 2011; Halsey and White, 2010). The majority of these studies suggest that dynamic body acceleration can serve as a reliable proxy of energy expenditure in active animals, especially in the context of terrestrial locomotion. Error estimates typically associated with the accelerometry method are similar to those of the heart rate method (Halsey et al., 2009). In fact, the accuracy of both methods is such that both estimate more accurately the energy expenditure of a group of animals, rather than that of individuals, as the algebraic error is typically considerably lower than the absolute error. However, the accelerometry method has its limitations that arise from the fact that it quantifies energy-consuming movements of animals, assuming that energy expenditure increases with movement intensity and duration. Accordingly, it works best if the energy expended during activity accounts for the majority of the overall energy budget of an animal. Periods of inactivity, when animals move little but might engage in energetically costly physiological processes (e.g. digestion, thermoregulation), will most likely not be picked up by the accelerometry method. Despite this, body acceleration was shown to be a significant predictor of energy expenditure in bantam chickens (*Gallus gallus*), even during periods of inactivity, albeit with much less accuracy than provided by the heart rate method (Green et al., 2009b). While this is perhaps surprising, significance was achieved by pooling data from various periods of inactivity (i.e. digestion and thermoregulation) during which there must have been sufficient movement, correlating with both PDBA and \dot{V}_{O_2} .

Considering the implications of this for our study with marine turtles, it is clear that thermoregulatory costs are of little importance to most of these reptiles. Apart from behavioural means (Hochscheid

et al., 2010), chelonid sea turtles generally do not thermoregulate and, hence, do not spend energy for thermoregulatory purposes. Leatherback turtles, on the other hand, might use the metabolic heat generated by vigorous swimming activity to maintain an elevated and stable body temperature (Bostrom and Jones, 2007; Bostrom et al., 2011). This, however, does not pose a problem for the accelerometry method. By contrast, energetic costs associated with the process of digestion would most likely go undetected by the accelerometry method. However, our turtles were not in a post-absorptive state during experimentation but were instead maintained on their normal feeding schedule, so that digestive costs are included in our respiratory measurements. We decided on this approach for two reasons. Firstly, it would have been impossible to maintain the animals in an unfed state over such a long period within our set-up, without causing severe disturbance. Secondly, green turtles at their foraging grounds, the main target of our future investigations, will most likely be in a comparable nutritional state (i.e. absorptive). One possible complication in this context is the basking behaviour occasionally observed in marine turtles. For loggerhead turtles, it was suggested that periods spent basking at the surface have a re-warming function to compensate for decreased body temperatures when diving in cooler water, possibly to enhance digestive function (Hochscheid et al., 2010). While ambient temperature is monitored by the acceleration data logger and was included in our model, it is not clear how well such temperature measurements will represent turtle body temperature (affecting turtle metabolism) under these circumstances. The relationship between PDBA and \dot{V}_{O_2} that we found in adult green turtles was not affected by activity status, indicating that body acceleration can be used to estimate energy expenditure even during periods of rest. Similar to the case of the bantam chickens (Green et al., 2009b), there must have been sufficient movement during resting periods of turtles (ascending into the chamber to breathe and descending again) for a correlation between PDBA and \dot{V}_{O_2} .

In contrast to most accelerometry studies to date, Halsey and colleagues (Halsey et al., 2011) found that body acceleration (ODBA) did not correlate with \dot{V}_{O_2} during single dive cycles of double-crested cormorants (*Phalacrocorax auritus*) diving to a depth of 5 m. A number of potential explanations were advanced for this missing correlation. One possibility is rooted in the methodological constraint of calculating metabolic rate in diving animals by measuring the amount of oxygen taken up between dives. If divers do not always replenish their oxygen stores to identical levels, then metabolic rate calculations based on single dive cycles will be erroneous, so that it is necessary to consider entire dive bouts (Fahlman et al., 2008b). Clearly, our turtles did not replenish their oxygen stores to identical levels with their single breaths between dives (Fig. 3; see Materials and methods). Hence, it was not possible to investigate dive costs and their association with dynamic body acceleration on the basis of single dive cycles. Accordingly, we considered periods as long as possible (typically ~1.5 h for each activity level) for our investigation. By doing so, we prevented erroneous metabolic rate calculations that might have concealed the correlation between PDBA and \dot{V}_{O_2} . Another potential explanation for the missing correlation in cormorants is linked to a difference in density of the two media that the birds moved in. Movement of the birds during diving might have been dampened by the greater resistance in water, so activity at the surface might have disproportionately affected ODBA. Marine turtles, by contrast, spend the majority of their time underwater with only brief periods at the surface and even then remain effectively submerged. They only break the surface with their head (and potentially the top of their carapace), which makes them less susceptible to problems associated with differences in the resistance of water and air, potentially affecting ODBA/PDBA (Halsey et al., 2011). In this

context it is of interest to note that a recent study successfully used accelerometry to estimate FMR in a fully aquatic species, the Australian cuttlefish (*Sepia apama*) (Payne et al., 2011). Hence, while the suitability of the accelerometry method to estimate energy expenditure during diving in endotherm divers awaits further investigation, our results suggest that accelerometry works well in aquatic reptiles.

LIST OF ABBREVIATIONS

FMR	field metabolic rate
f_R	respiratory frequency (breaths h ⁻¹)
LME	linear mixed effects model
M_b	body mass (kg)
ODBA	overall dynamic body acceleration (g)
PDBA	partial dynamic body acceleration (g)
$s\dot{V}_{O_2}$	mass-specific oxygen consumption rate (ml min ⁻¹ kg ^{-0.83})
T_w	water temperature (°C)
\dot{V}_{O_2}	oxygen uptake (ml)
\dot{V}_{O_2}	oxygen consumption rate (ml min ⁻¹)

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Caractéristiques maternelles, performances

et stratégies de reproduction

des tortues marines de Guyane



Résumé

Les organismes font face à des compromis entre leur reproduction, leur maintenance et leur survie, dont découlent des stratégies adaptatives énergétiques, comportementales et écologiques.

Ce travail de thèse propose de préciser les stratégies de reproduction chez la tortue luth *Dermochelys coriacea* nidifiant en Guyane. Nous avons étudié les caractéristiques maternelles, les performances de reproduction et les potentiels liens existants entre la migration et la reproduction chez une population d'individus d'identité connue, suivis grâce à un suivi longitudinal original combinant biométrie, physiologie et biologie moléculaire.

Premièrement nous montrons que les tortues luth opèrent comme des reproducteurs sur capital, i.e., leur reproduction repose sur les ressources stockées sous forme de réserves corporelles pendant la migration précédant la saison de ponte. D'autre part, nous suggérons que les femelles ajustent la durée de leur migration en fonction des conditions océanographiques rencontrées pendant la migration. Ceci leur permettrait, à l'échelle de la vie, de répondre au compromis entre la reproduction en cours et les reproductions futures. Enfin, notre démarche souligne l'importance de prendre en compte les caractéristiques individuelles dans la compréhension des stratégies de reproduction, et de manière ultime pour l'établissement de modèles réalistes de la dynamique des populations, notamment dans le cas d'espèces emblématiques telles que les tortues marines.

Mots-clés : tortues marines, stratégies de reproduction, compromis, tortue luth *Dermochelys coriacea*, suivi longitudinal, biométrie, physiologie, télomères, reproduction sur capital, modes de migration, conditions environnementales.

Abstract

Organisms face trade-offs between their reproduction, maintenance and survival, from which result adaptive strategies at the energetics, behavioural and ecological levels.

This PhD work investigates the reproductive strategies used by leatherback turtles, *Dermochelys coriacea*, nesting in French Guiana. We investigated maternal characteristics, reproductive output, and the possible links between migration and reproduction in a population of known identity, studied through a unique longitudinal monitoring, based on complementary approaches combining biometry, physiology and molecular biology.

First, we found that leatherback turtles are capital breeders, i.e. females' reproductive output displayed during their nesting season relies on body reserves previously stored during their migration. Second, we suggested that leatherback females adjust the duration of the migration according to the oceanographic conditions they experienced during migration. At a lifetime scale, this may allow females to face the trade-off between current and future reproductions. Finally, our approach highlights the importance to take into account individual characteristics in order to better understand reproductive strategies, and further assess realistic models of population dynamics, particularly when considering emblematic species such as sea turtles.

Key-words: sea turtles, reproductive strategies, trade-offs, leatherback turtle *Dermochelys coriacea*, longitudinal monitoring, biometry, physiology, telomeres, capital breeder, migration's patterns, environmental conditions.