The Behaviour of Free-living Marine Turtles: Underwater Activities, Migrations & Seasonal Occurrences

Corinne Sophie Martin (B.Sc.)

Submitted to the University of Wales, in fulfillment of the requirements

for the Degree of Doctor of Philosophy

University of Wales Swansea
2003

To my family and friends

SUMMARY

Chapter 1 presents the results of an investigation into the mid-water diving behaviour of Green turtles (*Chelonia mydas*) as they travelled back to Ascension Island. Time-Depth-Recorders (TDRs) and satellite transmitters were deployed onto five Green turtles, which were experimentally displaced. The profiles and possible functions of two types of mid-water dives were described. The results suggested that, as well as minimising predation by visual predators, both types of mid-water dives were likely to reflect some sort of resting behaviour at depth. Variable amounts of slow-speed swimming and some foraging activity (possibly on scyphozoans) may additionally have taken place during these dives.

Chapter 2 results from the examination of the vertical rates of movement during the mid-water dives performed by the five Green turtles studied in the first chapter. High-resolution Time-Depth-Recorders measured short-term variations in these rates. Because Green turtles dive with inflated lungs, short-term variations in descent and ascent rates were predicted to reflect tactics aimed at dealing with changes in lung volume, and hence buoyancy, with depth. Rates were found to be fast in the high buoyancy zone near the surface, but declined as lung volume, and hence positive buoyancy, declined.

Chapter 3 reports the findings gathered using Satellite-Relay-Data-Loggers (SRDLs) that had been deployed on four inter-nesting Green turtles at Ascension Island. For this population of Green turtles, it was the first time that one study provided simultaneously satellite locations, precise pressure information, as well as some estimates of swimming speed. It was attempted to confirm some of the direct and indirect results reported in previous studies, namely the depth utilisations (mainly 0-22 m), the spatially-restricted horizontal movements (less than a few km away from the main nesting beach) and the resting function of the dives to the sea bed (in addition to their predator- and/or surface turbulence avoidance function).

Chapter 4 tested whether Green turtle hatchlings routinely swam at the shallowest depths where the effects of the air/water interface would be minimised. This can be achieved, in theory, if animals swim submerged at a relative distance of at least 2.5-3 times their body depth (or maximum body thickness) below the surface. It was found that hatchlings tended to swim at about 3.5 times their maximum body thickness below the surface. This behavioural adaptation was predicted to increase survival rates by allowing hatchlings to maximise the distance from predator-rich coastal waters, before their limited energy reserves are exhausted.

In chapter 5, information regarding the temporal occurrence of Leatherback turtles (*Dermochelys coriacea*) in the Bay of Biscay (French Atlantic coast) was presented for 1979-2000. Annual incidences of live sightings and dead strandings were quite low from 1979 to the mid-nineties, in contrast to the relatively higher incidence thereafter. For the period 1979-2000, the temporal distributions of both dead standings and live sightings followed strong seasonal patterns. The results suggested that ecological and physical factors, such as the presence/absence of foraging material and SSTs, were probably major factors driving the seasonal patterns of Leatherback turtle occurrences in temperate waters.

DECLARATION

This work has not previously been accepted in substance for any degree and is not concurrently submitted in candidature for any degree.

Signed…………………………………………………(candidate)
Date……………………………………………………

STATEMENT 1

This thesis is the result of my own investigations, except where otherwise stated. A bibliography is appended.

Signed…………………………………………………(candidate)
Date……………………………………………………

STATEMENT 2

I hereby give consent for my thesis, if accepted, to be available for photocopying and for inter-library loan, and for the title and summary to be made available to outside organisations.

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CONTENTS

PREFACE

My arrival at the University of Wales, Swansea, in October 1999, was marked with mixed feelings of anticipation and excitement. Earlier that year, I had obtained an undergraduate Bachelor degree in Biological Sciences (with Microbiology), after having studied at the University of East Anglia (Norwich, U.K.). The mixed feelings I had upon my arrival in Swansea were probably due to the fact that I was about to start a doctoral training in the scientific field of behavioural ecology, which felt quite remote from the molecular biology-based subjects that I had been studying as an undergraduate student. However, this change of scientific orientation came at a price. The difficulty of obtaining funding became apparent, but my family kindly decided to fund my Doctorate degree.

After some discussion with my Ph.D. supervisor, Dr Graeme C. Hays, it was decided that my Doctorate was primarily going to be based on the analysis of diving and satellite-tracking data that would be obtained from free-ranging marine turtles. Hence, the aim of this thesis is to give new insights into the lives of freely diving marine turtles. Such datasets can reach substantial volumes, and there are usually many more topics to investigate, than time and people to do so. Because of a lack of funding, I was not planning to be involved in any of the fieldwork necessary for collecting these data. To start with I undertook a literature review, which helped me to assemble an extensive knowledge of diving in air-breathing marine vertebrates. The first piece of work I was involved with concerned the diving information collected using two satellite transmitters (models Telonics ST-6), attached to Green turtles (*Chelonia mydas*), migrating from Ascension Island to Brazil. Through this initial work, I became familiar with satellite tracking data and developed some data analysis skills, which I used during the rest of my Ph.D.. Some of the results of this work are included in the publication '*The diving behaviour of Green turtles undertaking oceanic migration to and from Ascension Island: dive durations, dive profiles and depth distribution*' (Hays *et al.* 2001a,). This publication also includes some diving information, which was derived from pressure data-loggers (Time-Depth-Recorders, or TDRs, plate 1, p. 6): I was also involved in the discussions regarding the relative depth at which animals, particularly migrating turtles, should routinely swim in order to minimise the negative effects of the air-water interface and wave drag. Unfortunately, this initial work was not substantial enough to form the basis of a chapter for my thesis.

This thesis takes the form of five chapters that are written as independent units. This was done in the hope that individual chapters will form the basis of manuscripts that may be published in the future. Although this has resulted in some repetition of literature between chapters, I preferred not to include an additional chapter that would summarise the up-to-date knowledge in the research fields touched on in this thesis. Instead, any relevant literature is directly mentioned within the text of the different chapters.

In chapter 1 (pp. 33-68), I used the diving information derived from pressure data-loggers and the location information obtained from satellite transmitters, both instruments being carried by Green turtles, in order to gain new insights into the mid-water diving behaviour of Green turtles during long-distance travel in the open ocean. In short, five Green turtles, nesting at Ascension Island, were the subject of an experiment aimed at testing their navigational and orientation abilities, through displacing them by ship, up to 270 km away from the island (plate 2, p. 6). Since pressure was sampled every 12 seconds by the TDRs during homing trips lasting up to 12 days, there was nearly 30 Mb of binary data to analyse (the homing trip of one of the turtles was described by 244,800 pressure measurements!). To process this huge volume of information I was introduced to the Minitab software, which allowed me to use keyboard commands (instead of mouse selection) and to write macros. The main outcome of this first chapter has been to shed light on the previously rather enigmatic functions of the mid-water dives performed by these turtles during long-distance travel.

The high-resolution pressure information derived from the TDRs also gave me the opportunity to investigate the descent and ascent tactics of Green turtles during these mid-water dives (in chapter 2, pp. 69-91). Indeed, Green turtles dive with inflated lungs (lungs are the main oxygen store), which make them positively buoyant upon leaving the surface, whilst buoyancy declines thereafter when lungs become compressed with increasing hydrostatic pressure. If transit costs are to be minimised, then turtles would be predicted to have evolved depth-sensitive descent and ascent tactics, with regards to changes in lung volume and buoyancy. I found that, in accordance with predictions, vertical movements are fast in the high buoyancy zone (near the surface), whilst they are slower as buoyancy declines with greater hydrostatic pressure. Using modelled lung volumes, I also showed that changes in lung volume, and hence buoyancy, are main factors driving the descent and ascent tactics during these mid-water dives.

Without much success, I then tried to explore ways of explaining the results obtained in chapter 2. A few months were spent in the attempt to elaborate a biomechanical model, based on the estimation of drag and buoyancy forces, using formulae and models described in the literature (e.g. Stephenson *et al.* 1989, Watson & Granger 1998). Much reading of Biomechanics textbooks had to be done to gain knowledge in what was, for me, an entirely new area of research. During most of that time, I remained unsure whether I was working in the right direction, or even if my model was correct. Fortunately, I finally met Dr John Videler (University of Groningen, The Netherlands), an internationally recognised expert in Biomechanics, during the Annual Meeting of the Society for Experimental Biology in Swansea (2002). His opinion was that the field data forming the basis of the model remained valuable, but the execution of experiments required to analyse this problem was ‘extremely difficult or even impossible, since all the forces involved had to be measured simultaneously’. Hence, with some regret, I have decided not to include this work in my thesis, although I do not regret having spent some time gaining some knowledge in Biomechanics, since I may work in this field in the future.

Although I was happy enough to continue with my data analysis-based Doctorate, I felt that my training as a scientist would not be complete if I was not involved in any of the fieldwork and data collection, not to mention the fact that, at the start of my Ph.D., I had yet to see a marine turtle. To become familiar with marine turtles, I visited the nesting beaches of Green and loggerhead marine turtles in Northern Cyprus in June 2000, and I was planning to visit the nesting beaches of Leatherback sea turtles (*Dermochelys coriacea*) in French Guiana, which I did in July 2002 (plate 3, p. 7). In the meantime, the research group, led by my Ph.D. supervisor, was preparing to go to Ascension Island (mid-Atlantic, plates 4, 5 & 6, p. 8-9) in May/June 2002, in order to deploy Satellite-Relay-Data-Loggers (or SRDLs, plate 7, p. 9) onto Green turtles, as part of a collaboration with the Sea Mammal Research Unit (St Andrews, Scotland). This was an opportunity not to be missed, so I wrote a research proposal in the hope of being awarded a Travelling Fellowship by the Journal of Experimental Biology (Cambridge, U.K.). My proposal was successful, allowing me to visit Ascension Island for one month. Because of my involvement in the fieldwork leading to the publication '*Bi-phasal long-distance migration in Green turtles*' (Hays *et al.* 2002b), I was included as one of the authors.

Chapter 3 (pp. 92-129) presents the results of the analysis I carried out on the diving information obtained from the SRDLs, which I helped deploy on Ascension Island in May/June 2002 (plate 8, p. 10). This is the first time that a satellite transmitter can provide, simultaneously, satellite locations and complete dive profiles, as well as swim speed for inter-nesting Green turtles at Ascension Island. In this chapter, I confirm some hypotheses made and results obtained in previous studies, for instance, depth utilisation, restricted horizontal movements and the function of U-shaped dives to the seabed. I then evaluate and discuss the aerobic dive limit of turtles resting at different depths, since the resting depth is closely linked with oxygen balance in this species.

Since adult Green turtles nest predominantly at night, I carried out a study during day-light hours, to determine the depth at which hatchling Green turtles swim. As I mentioned earlier, I had already been involved in the discussions regarding the relative depth at which aquatic animals should routinely swim, so that the negative effects of the air-water interface and wave drag are minimised. Although numerous studies quote the work of H. Hertel, a German naval engineer, to justify how far below the surface animals should swim to avoid wave drag, few studies have actually compared routine swimming depths with the body sizes of freely swimming animals. In chapter 4 (pp. 130-142), I report the results of the observation of more than 600 swimming dives performed by hatchling Green turtles during their swimming frenzy (plates 9 & 10, p. 11). Some of the observations were carried out in the *Turtle Pond* (plate 11, p. 12), as well as in English Bay. I discuss the results of my observation in the light of the predictions made from Hertel's work.

I felt that the analysis of the observational data, onto which chapter 4 was based, could be enhanced by including some relative values of wave drag. For this purpose, I used the water-flume facility of the Mechanical Engineering Department of the University of Wales, Swansea. The idea was to place inanimate objects of different sizes, at different depths below the water surface, whilst measuring total drag using a force transducer. Unfortunately, I did not manage to overcome some technical problems (such as controlling the buoyancy of the towed objects, or accurately measuring changes in the intensity of total drag) in time, before the water tunnel was eventually dismantled. Hence, none of this work is included in my thesis.

The final and fifth chapter (pp. 143-171) is the result of my collaboration with Dr Brendan J. Godley, a NERC Fellow at the University of Wales, Swansea. In 2001, he asked me whether I would be interested to take part in a project aimed at studying the long-term temporal and spatial occurrences of Leatherback sea turtles in European waters (Atlantic & Mediterranean). The project involved gathering as much sighting and stranding information as possible, from all available sources, and my task, as a native French speaker, was to collect sighting and stranding data published in the French scientific literature. Because I managed to collect more than a thousand records for the French Atlantic waters (1979-2000), Dr B.J. Godley and I decided that I should use this data as the basis of a chapter for my thesis. Since climatic fluctuations are known to influence the spatial and temporal distributions of many species, aquatic or terrestrial, both flora and fauna (Sims *et al.* 2001, Blenckner & Hillebrand 2002), I began my data analysis in this direction, by investigating potential long-term trends in the seasonal occurrence of Leatherback turtles in the Bay of Biscay (French Atlantic coast). However, I found that there was a lack of long-term trend in the year-to-year seasonal occurrences of Leatherback turtles, despite the Leatherback turtles being regular late-summer visitors to the Bay of Biscay, and despite the phenological changes reported for other animal species in western Europe (e.g. Ottersen *et al.* 2001, Walther *et al.* 2002). It remains to say, however, that even when analyses of long-term trends are based on excellent datasets (e.g. Huppop & Huppop 2003), phenological alterations (if there are any) are counted in (generally a few) days.

Finally, even though my doctoral research appears to have taken, sometimes, the occasional detours, these have nevertheless been very fruitful, since much knowledge and experience have been gained through these. As a final note, I would hope that some of what I have learned and discovered during my doctoral training may somehow benefit others when reading this thesis.

Plate 1. One of the Time-Depth-Recorders from CEFAS (Lowestoft, U.K.) that were used during the displacement experiments (Hays *et al.* 2001a).

Illustration 1. Un des ordinateurs de plongée (TDRs) venant de CEFAS (Lowestoft, R.U.), qui ont été utilisés pendant les expériences de déplacement de tortues par bateau (Hays *et al.* 2001a).

Plate 2. One of the Green turtles during the displacement experiments.

Illustration 2. Une des tortues Vertes, pendant les expériences de déplacement par bateau.

Plate 3. Nesting Leatherback sea turtles, in French Guiana (top photo: I am inserting a PIT-tag below the skin).

Illustration 3. Tortues Luths en train de nicher sur une plage de Guyane française (haut : je suis en train d'insérer une puce de marquage électronique sous sa peau).

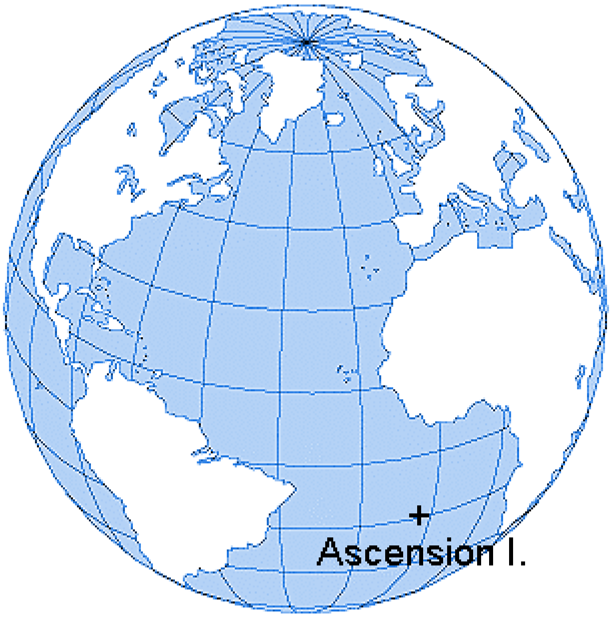

Plate 4. Ascension Island (7°47'S, 14°22'W).
Illustration 4. L'Ile de l'Ascension (7°47'S, 14°22'O).

Plate 5. View of Ascension Island, from Green Mountain.
Illustration 5. Vue d'Ascension, à partir de 'Green Mountain' (la montagne verte).

Plate 6. One nesting beach, close to Georgetown.
Illustration 6. Une des plages de ponte, près de Georgetown.

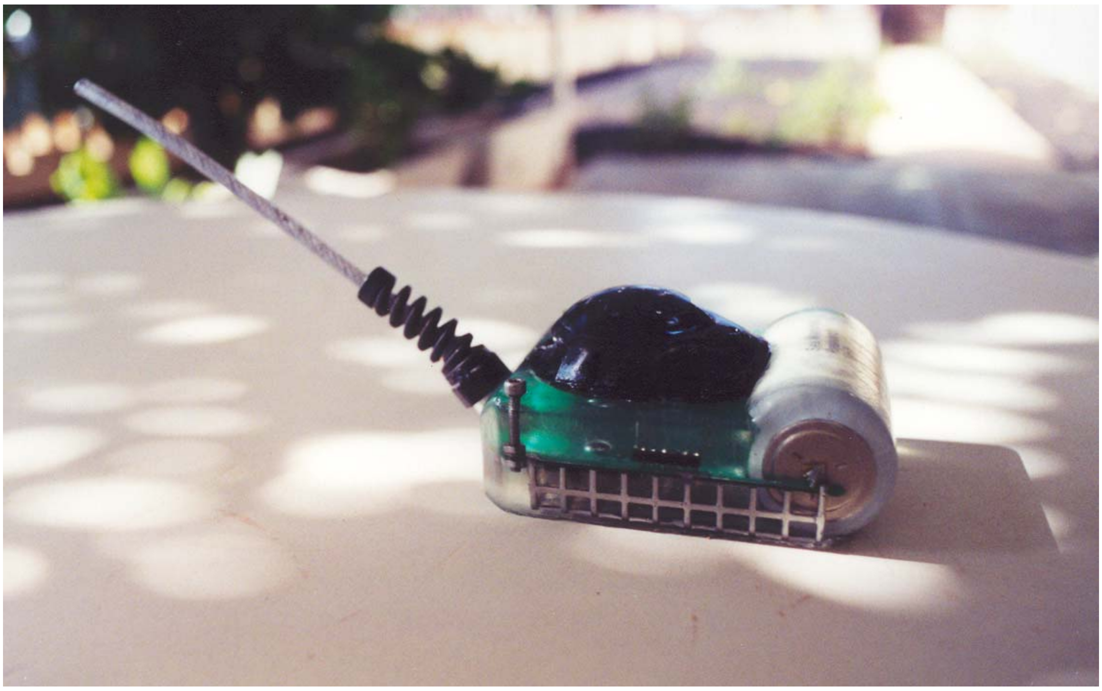

Plate 7. Satellite-Relay-Data-Logger (SRDL) from SMRU (U.K.).
Illustration 7. Transmetteur satellite (SRDL) venant de SMRU (R.U.).

Plate 8. After attachment of a SRDL, this Green turtle finishes covering its nest.
Illustration 8. Après la fixation d'un SRDL, cette tortue Verte finit de couvrir son nid.

Plate 9. A Green turtle hatchling.
Illustration 9. Une tortue Verte juste éclose.

Plate 10. In between observations of their swimming dives, hatchlings were kept in compartmented buckets.
Illustration 10. Entre les observations de plongées de nage pure, les tortues Vertes sont placées dans des boites compartimentées.

Plate 11. The *Turtle Pond*, were most of the observations dealt with in chapter 4 were carried out.

Illustration 11. Le *Réservoir aux Tortues*. Autrefois, il servait au stockage des tortues adultes, avant leur chargement sur des navires transatlantiques (ces tortues étaient gardées vivantes à bord, et servaient de réserves de nourriture).

PRÉFACE

Mon arrivée à l'Université du Pays de Galles, Swansea (R.U.), en Octobre 1999, a été marquée d'un sentiment de contentement mêlé d'une certaine appréhension. Quelques mois auparavant, j'avais obtenu un diplôme de Bachelor en Biologie (équivalent à la Maîtrise française), après avoir étudié à l'Université d'East Anglia (Norwich, R.U.). Mes sentiments à l'arrivée à Swansea étaient probablement dus au fait que j'allais débuter un Doctorat dans la spécialité scientifique d'écologie comportementale, ce qui semblait assez éloigné des sujets de biologie moléculaire, que j'avais étudiés jusqu'ici. Ce changement d'orientation scientifique n'a pas été sans prix, vu que ma famille et moi-même décidions de financer mon Doctorat, car il semblait difficile de trouver une autre source de financement.

Après avoir longuement discuté avec mon directeur de thèse, Dr G.C. Hays, il a été décidé que mon Doctorat allait être principalement basé sur l'analyse de données de profondeur et de données satellites, qui seraient obtenues à partir du comportement naturel de tortues marines. De ce fait, le but de cette thèse est de fournir de nouvelles connaissances concernant la vie des tortues marines dans leur environnement naturel. De telles bases de données peuvent atteindre des tailles considérables, et il y a habituellement plus d'aspects à étudier que de temps ou de personnes pour le faire. A cause d'un manque de financement, je n'étais pas sensée participer aux expéditions visant à collecter ces données. Pour commencer, j'ai entrepris une révision bibliographique, ce qui m'a permis d'assembler une connaissance assez étendue de la physiologie et du comportement de plongée des grands vertébrés marins. Mon premier sujet de recherche a été l'analyse de données obtenues à partir de deux transmetteurs satellites (modèles Telonics ST-6), qui avaient été fixés aux carapaces de deux tortues Vertes (*Chelonia mydas*), avant leur migration de l'Ile de l'Ascension (près de Saint Hélène, dans l'Océan Atlantique) jusqu'aux côtes du Brésil. A travers cette étude, je me suis familiarisée avec l'analyse de données satellites, et j'ai développé des compétences d'analyse de données et d'analyse statistique, qui m'ont servi durant le reste de ma thèse. Certains de ces résultats ont été inclus dans la publication '*The diving behaviour of green turtles undertaking oceanic migration to and from Ascension Island: dive* *durations, dive profiles and depth distribution*' (ou 'Le comportement de plongée de tortues Vertes, pendant leur migration vers et à partir de l'Ile de l'Ascension: temps de plongée, profils des plongées et distribution des profondeurs de plongée', Hays *et al.* 2001a). Cette publication comprend également des données de profondeur, qui ont été collectées séparément avec des ordinateurs de plongée, portés par d'autres tortues Vertes (ces instruments se nomment Time-Depth-Recorders, ou TDRs, illustration 1, p. 6). J'ai aussi pris part aux discussions concernant la profondeur relative, sous la surface de l'eau, à laquelle les grands vertébrés marins devraient nager, afin de réduire au mieux les effets de friction dus à la présence de l'interface eau-air. Malheureusement, cette recherche initiale n'a pas été de taille assez importante pour faire l'objet d'un chapitre de ma thèse.

Cette thèse est composée de cinq chapitres, qui ont été rédigés de manière indépendante, car j'espère qu'ils formeront la base de manuscrits qui pourront être publiés plus tard. Il est vrai que ce style a engendré quelques répétitions de littérature scientifique dans certains chapitres, mais j'ai toutefois préféré ne pas inclure un autre chapitre qui aurait rassemblé les connaissances scientifiques, publiées jusqu'à ce jour, concernant les domaines de recherche biologique couverts par cette thèse.

Dans le premier chapitre (pp. 33-68), j'analyse des données de profondeur obtenues à partir d'ordinateurs de plongée, en même temps que des données satellites obtenues à partir de transmetteurs satellites, ces instruments ayant été fixés sur des tortues Vertes d'Ascension. Cette analyse m'a permis de fournir de nouvelles connaissances concernant leur comportement de plongée pendant leurs voyages dans l'océan. En résumé, cinq tortues Vertes, qui avaient pondu sur l'Ile de l'Ascension, ont été les sujets d'une expérience visant à tester leur habileté à s'orienter et à naviguer dans l'océan, après avoir été transportées (270 km maximum), par bateau, à distance de l'Ile où elles avaient été capturées (illustration 2, p. 6). Comme les ordinateurs de plongée avaient été programmés pour calculer la profondeur des tortues toutes les 12 secondes pendant leur voyage de retour (une des tortues a mis plus de 10 jours pour retourner sur l'Ile), cette expérience a fourni presque 30 Mo de données à analyser (le voyage de retour d'une des tortues comprenait 244 800 mesures de profondeur de plongée). De façon à analyser cette énorme quantité de données, j'ai dû apprendre à me servir du logiciel Minitab d'analyse statistique, ce qui m'a permis d'utiliser des commandes au clavier (au lieu de sélectionner à l'aide de la souris) et d'écrire des petits programmes d'analyse. La principale conclusion de ce premier chapitre a été de préciser le rôle, auparavant plutôt énigmatique, des plongées à mi-eau, que font les tortues Vertes pendant leurs longs voyages à travers l'océan.

Les données de profondeur, obtenues à partir de TDRs, étaient de haute précision, ce qui m'a permis d'examiner, dans le second chapitre (pp. 69-91), les stratégies de descente et de remontée pendant les plongées à mi-eau du premier chapitre. En effet, les tortues Vertes sont connues pour avoir leurs poumons remplis d'air pendant ces plongées à mi-eau (les poumons sont leur principale réserve d'oxygène sous la surface). De ce fait, les tortues présentent une flottabilité substantielle au moment où elles quittent la surface, tandis que l'on peut prédire que leur flottabilité diminuera lorsque leurs poumons se comprimeront, en même temps que la pression hydrostatique augmentera. Si le but est de minimiser le coût de déplacement entre la surface et la profondeur maximale des plongées, on peut prédire que les tortues ont élaboré des tactiques visant à compenser les changements de volume pulmonaire, et donc de flottabilité, en fonction de la profondeur. Le résultat de cette analyse a montré que les mouvements verticaux sont rapides dans la zone de grande flottabilité (près de la surface), tandis qu'ils deviennent progressivement plus lents quand la pression hydrostatique augmente. En utilisant une modélisation des volumes pulmonaires, j'ai également montré que les variations des volumes pulmonaires, et donc de flottabilité, sont les facteurs principaux dans la détermination des stratégies de descente et de remontée pendant ces plongées à mi-eau.

Sans trop de succès, j'ai ensuite essayé d'expliquer le mécanisme exact derrière les stratégies décrites dans le second chapitre. Plusieurs mois ont passé, pendant lesquels j'ai tenté d'élaborer un modèle biomécanique, basé sur l'estimation des forces de friction et de flottabilité à partir de formules et de modèles déjà publiés (par exemple Stephenson *et al.* 1989, Watson & Granger 1998). Je me suis plongée dans des livres de Biomécanique afin d'obtenir une connaissance dans ce qui était, pour moi, un tout nouveau domaine de recherche. Pendant ces mois-ci, je n'étais pas certaine de travailler dans la bonne direction, ou même de l'exactitude de mon modèle. Heureusement, j'ai finalement fait la rencontre de Dr John Videler (Université de Groningen, Pays-Bas), un expert en Biomécanique, pendant la réunion annuelle de la Société de Biologie

Expérimentale à Swansea (2002). Son opinion sur ma recherche a été que les données de profondeur restent très intéressantes, mais que les expériences nécessaires pour analyser ce problème 'sont extrêmement difficiles, voire impossibles, à effectuer parce que toutes les forces impliquées doivent être mesurées simultanément'. Ainsi, avec certains regrets, j'ai décidé de ne pas inclure cette modélisation dans ma thèse, même si je ne regrette pas d'avoir passé un certain temps à m'initier à la Biomécanique, car j'y retournerai peut être dans le futur.

Même si j'étais plutôt heureuse de continuer mon Doctorat comme il était prévu au départ, je sentais que mon apprentissage scientifique ne serait pas complet si je ne m'impliquais pas plus dans le travail sur le terrain et dans la collecte de données (inutile de préciser qu'avant le début de ma thèse, je n'avais jamais vu de tortues marines). De façon à devenir plus familière avec les tortues de mer, j'ai visité, en juin 2000, les sites de ponte de tortues Vertes et Caouannes en Chypre du Nord, et je prévoyais de visiter les sites de ponte de tortues Luth (*Dermochelys coriacea*) en Guyane française, ce que j'ai fait en juillet 2002 (illustration 3, p. 7). Il restait que le groupe de recherche, mené par mon directeur de thèse, se préparait à aller sur l'Ile de l'Ascension (illustrations 4, 5 & 6, p. 8-9) en mai/juin 2002. Le but était de fixer des transmetteurs satellites (SRDLs, illustration 7, p. 9) sur des tortues Vertes, dans le cadre d'une collaboration avec l'unité de recherche sur les mammifères marins (Sea Mammal Research Unit, SMRU, St Andrews, Ecosse). C'était une occasion à ne pas manquer, et j'ai donc rédigé une proposition de projet de recherche dans l'espoir d'obtenir une des bourses de recherche offertes par le Journal et par la Société de Biologie Expérimentale (Cambridge, R.U.). Cette proposition de recherche a été acceptée, ce qui m'a permis de financer mon séjour sur l'île. Parce que j'ai été très impliquée dans le travail de terrain sur Ascension, cette tâche m'a valu d'être un des auteurs sur la publication '*Bi-phasal long-distance migration in green turtles*' (ou 'Migration de longues distances, en deux phases, par des tortues Vertes', Hays *et al.* 2002b).

Le troisième chapitre (pp. 92-129) présente les résultats de mon analyse de données de profondeurs obtenues à partir de des transmetteurs satellites, que j'ai aidés à fixer à Ascension en mai/juin 2002 (illustration 8, p. 10). C'est, en effet, la première fois qu'un transmetteur satellite fournit, de manière simultanée, des données satellites et des profils complets de plongées, ainsi que des données sur la vitesse de nage, pour des tortues Vertes d'Ascension. Dans ce chapitre, je confirme certaines hypothèses avancées et certains résultats obtenus au cours d'autres études sur leur comportement pendant l'intervalle de temps entre deux pontes, en particulier leurs déplacements horizontaux, leur utilisation des profondeurs, et le rôle des plongées en forme de U sur le fond de la mer. Ensuite, j'évalue et discute les durées limites de plongée aérobique de tortues Vertes se reposant à des profondeurs différentes, car les réserves d'oxygène sont très liées aux profondeurs de repos pour cette espèce.

Parce que les tortues Vertes pondent surtout la nuit, j'ai profité des heures de jour à Ascension pour effectuer une étude qui visait à déterminer à quelle profondeur les tortues Vertes juste écloses nagent. Comme je l'ai mentionné plus haut, j'avais déjà pris part aux discussions concernant la profondeur relative, sous la surface de l'eau, à laquelle les grands vertébrés marins devraient nager, afin de réduire au maximum les effets de friction dus à la présence de l'interface eau-air. Bien que de nombreuses études mentionnent le travail de H. Hertel, un ingénieur naval allemand, pour justifier à quelle profondeur, sous la surface, les grands vertébrés devraient nager afin d'éviter de telles forces de friction, peu d'études ont vraiment comparé les profondeurs de nage avec les dimensions des animaux en question. Dans le quatrième chapitre (pp. 130-142), je rends compte de l'observation de plus de 600 plongées de nage pure, faites par des tortues Vertes juste écloses (illustrations 9 & 10, p. 11). Certaines des observations ont été faites dans le Réservoir aux Tortues (illustration 11, p. 12), et le reste dans une baie abritée (la Baie des Anglais). Je discute les résultats de mes observations dans le cadre des prédictions faites à partir de la recherche d'Hertel.

Je sentais que l'analyse des observations, sur lesquelles le quatrième chapitre est basé, pourraient être complétées par des estimations de forces de frictions. Dans ce but, j'ai utilisé le tunnel d'eau du département d'Ingénierie Mécanique de mon Université. L'idée principale était de placer des objets de tailles différentes, à des profondeurs différentes sous la surface de l'eau du tunnel, tout en mesurant les forces de friction. Malheureusement, je n'ai pas réussi à résoudre quelques difficultés techniques (problèmes de flottabilité des objets, mesure précises des frictions) à temps, avant que le tunnel ne soit démantelé. Ainsi, rien de cette expérience n'est inclus dans ma thèse.

Le cinquième et dernier chapitre (pp. 143-171) est le résultat d'une collaboration avec Dr Brendan J. Godley, un chercheur post-doctoral de l'Université du Pays de

Galles, à Swansea. En 2001, il m'a demandé si je voudrais participer à un projet visant à étudier les distributions temporelles et spatiales des tortues Luth dans les eaux européennes (Atlantique et Méditerranée). Le projet visait à compiler autant d'observations de tortues vivantes ou mortes qu'il serait possible de trouver, et ma tâche, en tant que française d'origine, a été de compiler les observations publiées dans la littérature scientifique française. Parce que j'ai réussi à rendre compte de plus de mille observations de tortues Luth sur la côte atlantique de France (1979-2000), Dr B.J. Godley et moi-même avons décidé que je devrais utiliser ces données pour un chapitre de ma thèse. Comme les fluctuations climatiques sont un facteur reconnu dans la distribution temporelle et spatiale de beaucoup d'espèces, aquatiques ou terrestres, la faune comme la flore (Sims *et al.* 2001, Blenckner & Hillebrand 2002), j'ai commencé mon analyse dans cette direction, en recherchant des tendances à long-terme dans la distribution saisonnière des tortues Luth dans le Golfe de Gascogne. Cependant, j'ai trouvé que, bien que les tortues Luth soient présentes très régulièrement dans le Golfe de Gascogne à la fin de chaque été, la base de données n'a pas permis de mettre en évidence une tendance d'évolution à long-terme concernant leurs distributions saisonnières, année après année, ceci malgré les changements phénologiques qui ont été reportés pour d'autres espèces d'Europe de l'ouest (par exemple, Ottersen *et al.* 2001, Walther *et al.* 2002). Il reste à dire, néanmoins, que même lorsque les analyses de tendances à long-terme sont basées sur d'excellentes bases de données (par exemple Huppop & Huppop 2003), les altérations phénologiques (si elles existent) se comptent généralement en (quelques) jours.

Pour finir, même si mon Doctorat semble avoir fait, parfois, certains détours, je reste persuadée que ces détours ont néanmoins été très fructueux, spécialement parce que connaissance et expérience ont été acquises à travers eux. Somme toute, j'espère que ce que j'ai moi-même appris et découvert pendant mon Doctorat pourra être utile à d'autres à travers cette thèse. C'est une des raisons pour lesquelles cette préface est traduite dans ma langue maternelle, ainsi que les résumés de chacun des cinq chapitres (pp. 28-32).

ACKNOWLEDGEMENTS

My thanks must go first to my Ph.D. supervisor, Dr G.C. Hays, whom I am greatly indebted to, in particular for letting me begin a doctoral training in a field of biological research which I was previously not familiar with. I have learned a lot from him, and his guidance and advice have immensely helped me throughout the years I have spent in Swansea.

Secondly, I would like to express my gratitude to my family, especially for the considerable trust they had in my capabilities: their confidence in me was generally much more extended than the trust I had in my own capabilities. Their moral and emotional supports have been priceless, whilst their financial support remains invaluable.

Finally, from fear of forgetting any of the other people whom I am deeply indebted to, I would simply say that I owe them more than they would think, and that I would not have made it here without them. To all of you, thank you for your advice, for your helping hands during fieldwork and at Swansea, for the time you spent reading and commenting on my work, and above all, for your generosity and the moral support you showed towards me.

Chapters 1 & 2.

I thank B.J. Godley (University of Wales Swansea; UWS), F. Glen (UWS), A.C. Broderick (UWS), S. Akesson (Lund University, Sweden), J.D. Metcalfe (CEFAS, U.K.), P. Luschi (University of Pisa, Italy), F. Papi (University of Pisa), H. H. Geoffrey Fairhurst (Administrator for Ascension Island), the First Ascension Scout Group and island residents, the United States Air Force, the Royal Air Force, Merlin Communications, CRS, Sealift and the master and crew of the *MV Ascension*. This work was supported by grants awarded to G.C. Hays from the Natural Environmental Research Council of the UK (NERC) and from the Department of the Environment, Transport and Regions (DETR) through their Darwin Initiative programme.

Chapters 3 & 4.

I thank B.J. Godley (UWS), A.C. Broderick (UWS), S. Richardson (UWS), R. Frauenstein, J. Henshaw, and H. H. Geoffrey Fairhurst (Administrator for Ascension Island). The work was supported by NERC, the Department of the Environment, Food and Rural Affairs (DEFRA), the Foreign & Commonwealth Office Environment Fund for the Overseas Territories, the Society for Experimental Biology and the DETR.

Chapter 5.

I would like to express my gratitude to Dr Raymond Duguy (Muséum d’Histoire Naturelle de La Rochelle, France) and to Professeur Claude Martin (Université d’Aix-Marseille II, France), for providing me with numerous reprints of the publications used for this study. I also thank B.J. Godley for his advice and time. Thanks to Bob Dattore (COADS) for providing the SST data, and to the California Institute of Technology (NASA/JPL PO.DAAC) for providing free access to AVHRR imagery.

REMERCIEMENTS

Mes remerciements se doivent de revenir, en premier, à mon directeur de thèse, Dr G.C. Hays, à qui je dois beaucoup, en particulier pour m'avoir permis de commencer une thèse doctorale dans une spécialité de recherche biologique, qui m'était tout à fait inconnue. Ses conseils m'ont énormément aidée et faite avancer pendant ces années passées à Swansea.

Ensuite, je voudrais exprimer mon immense gratitude à l'égard de ma famille, particulièrement pour avoir eu tant confiance en moi. Leur soutien moral a été inestimable, tandis que leur assistance financière demeure irremplaçable.

Enfin, de peur d'oublier même une des personnes qui m'ont tellement aidée, je voudrais simplement dire que je leur dois plus qu'elles ne l'imaginent, et que je ne serais pas arrivée jusqu'ici sans elles. Merci à vous tous pour vos conseils, pour votre aide pendant le travail sur le terrain et à Swansea, pour le temps que vous avez passé à lire et commenter mes travaux, et surtout, pour votre générosité et vos encouragements.

INTRODUCTION

The lives of marine turtles consist of an almost continuous series of migrations, from the off-shore migration of newly hatched nestlings to the migrations of adults between foraging and breeding sites (Lohmann *et al.* 1997). Migration in marine turtles may be considered the central theme of the present thesis since all five chapters are more or less directly connected with this topic. In chapter 1 and 2, the diving behaviour of adults during long-distance travel was investigated, while in chapter 3, it was the diving behaviour of adult turtles during one portion of their breeding migration that was explored. In chapter 4, the swimming behaviour of newly emerged hatchlings was studied, whilst chapter 5 finally looked at the seasonal occurrences of migrating adults.

Marine turtles are basically creatures that spend their entire juvenile and adult lives at sea, except for the brief time female adults spend on the beach to nest. For logistical reasons, however, the study of marine turtles has historically focused on aspects of their biology, which are tied to the land, e.g. nesting activities and hatchling success, or which can be studied in the laboratory, e.g. locomotion of hatchlings and respiration physiology. Meanwhile, marine turtles are long-distance migrants and are amongst the longest and deepest divers of the air-breathing vertebrates and, in the wild, most marine turtles spend as little as 3 to 6 % of their time at the surface (Lutcavage & Lutz 1997). Such aspects of their at-sea biology are difficult, or even impossible, to study or re-create in the laboratory, hence making it important to know about the lives of free-ranging turtles. Although visual information can sometimes be adequate for the study of free-living marine turtles (chapter 4 and 5 illustrated this option), the advent of small recording and/or transmitting devices that can be directly attached on free-living turtles has revolutionised the study of marine turtles in their natural environment (chapter 1, 2 and 3 provided examples of their use).

The first chapter (pp. 33-68) of this thesis presents the result of an investigation into the mid-water diving behaviour of Green turtles as they travelled back to Ascension Island. Time-Depth-Recorders (TDRs) and satellite transmitters were deployed onto five Green turtles, which were experimentally displaced. Mid-water diving (i.e. diving activity deeper than 6 m) showed a clear diel pattern, with turtles mostly showing this activity during night-time, whilst more time was allocated to sub-surface travelling dives in day-time. The speed of travel, as estimated from the satellite locations, declined when the proportion of time engaged in mid-water diving increased, i.e. when the proportion of time spent performing type 1 and 2 mid-water dives increased. The profiles of these two types of mid-water dives, whose shapes are specific to reptiles, presented a fast descent, then a gradual ascent phase, followed by a fast ascent to the surface. The type 2 dives also included a deeper excursion before the start of the gradual ascent. Their actual functions had remained enigmatic so far as marine turtles were concerned; therefore, the principal aim of this chapter was to give new insights into the function of these mid-water dives.

For most turtles in this study, there was a temporal change in the mid-water diving activity when turtles became engaged in the final, island-directed legs of their homing trips, as if the turtles had made contact with the island (e.g. *via* olfactory or auditory cues). During these legs, type 1 and 2 dives tended to be deeper and of shorter duration, than during other times of their homing trips. In contrast to type 2 dives and other mid-water dives, which could take place at any time during the diel cycle, type 1 dives occurred mostly at night. Type 2 dives and other mid-water dives could reach depths of up to 60 m and appeared to take place mostly at the start and/or at the end of homing trips.

The results suggested that, as well as minimising the time spent at the surface and thus the attacks by visual predators or any turbulence at the surface, both type 1 and 2 dives were likely to reflect some sort of resting behaviour at depth. Additionally, variable amounts of slow-speed swimming may have taken place in an energy-efficient manner during the gradual ascent. Some foraging activity (possibly on scyphozoans) could also take place during these mid-water dives. The examination of dive intervals suggested that these dives remained in the turtles' aerobic range. These mid-water dives may have provided opportunities to scan the water column, as part of a searching behaviour, especially during the deeper excursions presented by type 2 dives. It was concluded that bouts of mid-water diving may have offered an alternative to stopping horizontal movement for resting purposes (stopping horizontal movement would result in an increase of the long-term cost of basal metabolism). Slow-speed swimming would permit to keep these basal metabolic costs down, as well as providing a certain amount of rest, preferentially at night (because of the intrinsic diurnal activity cycle in this species).

The second chapter (pp. 69-91) of this thesis results from the examination of the vertical rates of movement during the mid-water dives performed by the five Green turtles studied in the first chapter. High-resolution Time-Depth-Recorders measured short-term variations in these rates. Descent and ascent rates of vertical movements revealed changes that were similar in pattern to changes in hydrostatic pressure with depth. Because Green turtles are shallow-divers, submerging with inflated lungs (their main oxygen store underwater), it was predicted that the short-term variations in descent and ascent rates would reflect tactics aimed at dealing with changes in lung volume and hence buoyancy with depth. Typically, descent rates were fast in the high buoyancy zone upon leaving the surface, but as the dive continued, descending movement progressively decelerated as up-thrust declined. When deeper than the hypothesised depth of neutral buoyancy (19 m at the deepest), descent rates seemingly became independent from depth. This change in behaviour around 19 m provided additional support for the hypothesis that Green turtles from Ascension may attain neutral buoyancy around 19 m if they left the surface with fully inflated lungs.

During ascent, rates progressively accelerated (until shortly before surfacing), in line with the gradual increase in up-thrust. Finally, modelled changes in mass-specific lung volumes (used as indicator of buoyancy) showed a positive relationship with short-term variations in descent and ascent rates, with rates being faster when up-thrust became greater. During descent, this behavioural adaptation was predicted to help minimise the proportion of time spent fighting up-thrust, whilst ascending movement was predicted to be mostly passive through using the buoyant lift of expanding lungs.

While chapter 1 and 2 shed light into the behaviour of travelling marine turtles, chapter 3 (pp. 92-129) reports the findings gathered on inter-nesting Green turtles at Ascension Island. Satellite-Relay-Data-Loggers (SRDLs) were deployed on four Green turtles in order to study their diving responses and movements during the inter-nesting period. For this population of Green turtles, it was the first time that one study provided simultaneously satellite locations, precise pressure information, as well as some estimates of swimming speed. The satellite transmitters carried micro-processors, which were programmed to compress pressure information in such a way that complete profiles of dives deeper than 6 m could be reconstructed. It was attempted to confirm some of the direct and indirect results reported in previous studies, namely the depth utilisations (mainly 0-22 m), the spatially-restricted horizontal movements (less than a few km away from the main nesting beach) and the actual function of the dives to the sea bed (in addition to their surface- and thus predator- and/or surface turbulence avoidance function).

Using the swim speed information obtained from one turtle, these dives to the sea bed were shown to be resting dives, during which turtles are thought to be neutrally buoyant during the bottom phase. Since resting dives were rarely deeper than 19 m, this provided further support for 19 m being the maximum depth at which Green turtles from Ascension Island may attain neutral buoyancy. Resting depths being closely linked with dive duration and oxygen balance in this species, lung volumes were modelled in order to estimate the aerobic dive limit (ADL) of turtles resting at different depths. It was found that turtles rarely approached their physiological limits during resting dives because there was a large variation in dive duration for similar resting depths, i.e. for similarly-sized oxygen stores.

Whilst the first three chapter dealt with adult turtles, the fourth chapter (pp. 130-142) examines the results of an investigation into the swimming behaviour of hatchling Green turtles at Ascension Island, during their swimming frenzy. Animals swimming near a water/air interface may generate surface waves, and the energetic cost of creating and propagating these surface waves is predicted to increase transport costs. It might be expected that air-breathing animals would attempt to minimise the wave drag associated with surface waves, since this would reduce the associated energetic costs. This can be achieved, in theory, if such animals swim submerged at a relative distance of at least 2.5-3 times their body depth (or maximum body thickness) below the surface. Because of a lack of empirical data in the published literature for routine swimming depths, the depth of more than 600 swimming dives performed by 47 Green turtle hatchlings during their swimming frenzy was measured (by direct observation). It was found that hatchlings tended to swim about 7 cm below the surface, which roughly equated to 3.5 times their maximum body thickness. This behavioural adaptation was predicted to increase survival rates by allowing hatchlings to maximise the distance from predator-rich coastal waters, before their limited energy reserves are exhausted.

In contrast with the first four chapter, the final and fifth chapter (pp. 143-171) considers another species of marine turtles, the Leatherback turtle, and was based on a dataset gathering information on a comparatively higher number of individuals, i.e. at the population level more than at the individual scale. Indeed, information regarding the temporal occurrence of Leatherback turtles in the Bay of Biscay (French Atlantic coast) was presented for the period 1979-2000. A total of 1249 sighting and stranding reports for this species was compiled for the entire French Atlantic coast from published sources. Annual incidences of live sightings and dead strandings for a sub-area of the Bay of Biscay (centred around La Rochelle) were quite low from 1979 to the mid-nineties, in contrast to the relatively higher incidence thereafter. The incidence of live sightings for any one year was found to be positively correlated with the incidence of dead strandings. For the period 1979-2000, the temporal distributions of both dead standings and live sightings followed strong seasonal patterns, although dead strandings tended to peak later in the year (October) than live sightings (August), and dead strandings tended to be reported during most months of the year (whilst live sightings were mainly reported for June-October).

The peak occurrence of live sightings tended to coincide with the months of warmest Sea Surface Temperatures (SSTs) in the area, with 85% of live sightings in the study area occurring during months when SSTs were warmer than 18°C. There was a lack of phenological changes in the timing of occurrence, probably due to the low resolution of the dataset. The results suggested that ecological and physical factors, such as the presence/absence of foraging material and SSTs, were probably major factors driving the seasonal patterns of Leatherback turtle occurrences in temperate waters. The results of this study were discussed in the context of the results of previous studies on Leatherback turtles, in this area and elsewhere.

The main conclusion that can be drawn from this thesis is that free-living marine turtles tend to adapt their behaviour to the conditions and environments in which they evolve. The risk of predation has appeared to be a major factor influencing their diving and swimming behaviours. For example, in chapters 1 and 3, the mid-water dives and the dives to the sea bed allow adult turtles to obtain a certain amount of rest in an environment that is safer from predator attacks than would be the water surface. Another example is in chapter 4, where swimming at around three times their body depth below the surface decreases wave drag, and increases the hatchlings' chances of survival by maximising the distance travelled away from predator-rich coastal waters. In chapter 2, turtles have apparently managed to conciliate diving with inflated lungs with life in an environment where pressure varies substantially. Finally, turtles seem capable to time their long-distance migrations in order to be present in certain geographical areas when sea temperatures are warm enough and/or when their foraging material is widely available, whilst turtles are comparatively absent at other times of the year. Therefore, the behavioural adaptations of sea turtles, which were reported in this thesis have resulted from a complex combinations of factors of different natures, but whether these factors are of biological or physical nature, such behavioural adaptations are predicted to result in increased chances of survival of marine turtles.

RESUMES DES CHAPITRES

CHAPITRE 1: *Le comportement de plongée à mi-eau par des tortues Vertes, après une expérience de déplacement.*

Des ordinateurs de plongée (Time-Depth-Recorders, TDRs), ainsi que des transmetteurs satellites ont été fixés sur cinq tortues Vertes dans le but d'étudier leur comportement pendant des plongées à mi-eau, alors qu'elles retournaient vers l'Ile de l'Ascension, après une expérience de déplacement par bateau. Les plongées à mi-eau (c'est à dire à des profondeurs de plus de 6 m), étaient caractérisées par une claire alternance jour-nuit, les tortues passant beaucoup plus de temps à effectuer ces plongées pendant la nuit, tandis que pendant le jour, elles s'engageaient de préférence dans des plongées de nage pure, juste sous la surface de l'eau. La vitesse de déplacement, estimée à partir des positions satellites, avait tendance à ralentir lorsque le temps passé à plonger à mi-eau était plus important. Les profils des plongées de types 1 et 2, dont les formes sont spécifiques des reptiles, présentaient une descente rapide, puis une remontée lente, suivie d'une remontée rapide jusqu'à la surface de l'eau. Le type 2 présentait une excursion plus profonde avant le début de la remontée lente. Jusqu'ici, le but de ces types de plongées à mi-eau par des tortues marines était resté plutôt énigmatique.

Durant cette étude, un changement temporel a été détecté dans le comportement de plongée à mi-eau lorsque les tortues s'engageaient dans les dernières lignes droites (dirigées vers l'île) de leurs voyages de retour. Durant ces dernières lignes droites, les plongées de type 1 et 2 sont devenues plus profondes et ont duré moins longtemps qu'à d'autres moments des voyages de retour. Au contraire des plongées de type 2 et des autres plongées à mi-eau (toutes deux s'effectuant à n'importe quelle heure du jour), les plongées de type 1 étaient surtout de nature nocturne. Les plongées de type 2 (et les autres plongées à mi-eau) ont montré une tendance à prendre place au début et/ou à la fin des voyages de retour, et leurs profondeurs pouvaient atteindre 60 m. L'analyse des résultats a suggéré que les plongées de type 1 et 2 étaient susceptibles de minimiser les attaques de surface par des prédateurs visuel (et/ou de minimiser les effets des turbulences de surface) et, sans doute, reflétaient un comportement de repos sous l'eau. Des quantités variables de mouvement horizontal pourraient aussi prendre place, de façon économique, durant la remontée lente de ces plongées. Pendant ces plongées, il est aussi peut-être possible que les tortues se nourrissaient de scyphozoaires (méduses). Ces plongées à mi-eau pourraient également permettre aux tortues d'inspecter leurs environs, dans le cadre d'un comportement de prospection, particulièrement pendant les excursions plus profondes des plongées de type 2. Pendant les longs voyages à travers l'océan, ces plongées de repos, pendant lesquelles les tortues ne s'arrêteraient pas tout à fait de nager, permettraient aux tortues de se reposer sans toutefois augmenter leurs dépenses énergétiques journalières de base de façon significative.

CHAPITRE 2: *Les tactiques de descente et de remontée pendant les plongées à mi-eau de tortues Vertes.*

Des ordinateurs de plongée à haute résolution (Time-Depth-Recorders, TDRs) ont été utilisés dans le but d'examiner les vitesses verticales de mouvement, pendant les plongées à mi-eau de tortues Vertes, alors qu'elles retournaient vers l'Ile de l'Ascension, après une expérience de déplacement par bateau. Pendant les plongées à mi-eau (c'est à dire à des profondeurs de plus de 6 m), les changements de vitesses verticales au cours des descentes et remontées étaient semblables aux variations de pression hydrostatique en fonction de la profondeur dans l'eau. Parce que les tortues Vertes ne plongent pas très profond et quittent la surface avec des poumons remplis d'air (les poumons sont leur principale source d'oxygène sous l'eau), on peut prédire que les changements de vitesse verticale vont refléter des tactiques visant à compenser au mieux les variations de volume pulmonaire (compression, ré-expansion), et par conséquent, les variations de niveau de flottabilité, en fonction de la profondeur dans l'eau.

Les vitesses verticales de descente étaient rapides dans la zone de grande flottabilité (c'est à dire en quittant la surface), tandis que le mouvement de descente avait tendance à ralentir progressivement, en même temps que la profondeur dans l'eau augmentait et la flottabilité diminuait. Lorsque les tortues se trouvaient au dessous de la profondeur à laquelle leur flottabilité est théoriquement nulle (au plus profond 19 m), les vitesses verticales de descente semblaient devenir indépendantes de la profondeur dans l'eau. Ce changement de comportement autour de 19 m soutient l'hypothèse comme quoi les tortues Vertes d'Ascension obtiennent une flottabilité nulle, à peu près à 19 m, si elles ont quitté la surface avec leurs poumons complètement gonflés. Les vitesses verticales de remontée avaient tendance à accélérer progressivement (jusqu'à un plateau juste avant de percer la surface), en ligne avec l'augmentation graduelle de flottabilité due à la ré-expansion pulmonaire.

La modélisation des changements de volumes pulmonaires (utilisés comme indicateurs du niveau de flottabilité) a montré qu'il existait une relation positive entre les changements de volume pulmonaire et les changements de vitesses verticales pendant les descentes et les remontées: les vitesses verticales étaient plus rapides quand la flottabilité était plus élevée. Pendant les descentes, cette adaptation comportementale aidait la réduction du temps passé à nager contre la flottabilité, tandis que les mouvements de remontée pouvaient être plus ou moins passifs s'ils étaient facilités par la flottabilité due à l'air contenu dans les poumons.

CHAPITRE 3: *Le comportement de plongée de tortues Vertes à Ascension pendant l'intervalle de temps entre deux pontes.*

Sur l'Ile de l'Ascension, quatre transmetteurs satellites (Satellite-Relay-Data-Loggers, SRDLs) ont été fixés sur des tortues Vertes dans le but d'étudier leurs comportements de plongée et leurs mouvements pendant l'intervalle de temps entre deux pontes. Pour cette population de tortues Vertes, c'est la première fois qu'une étude a procuré, simultanément, des positions satellites, des informations de plongée, ainsi que des estimations de vitesse de nage (bien que seulement une tortue ait fourni des vitesses de nage). Les transmetteurs satellites contenaient des puces électroniques programmées pour compresser les informations de plongée de manière à pouvoir ultérieurement reconstruire les profils de plongées (ces plongées devaient être au moins à 6 m de profondeur). Les mouvements horizontaux à petite échelle (au plus loin à quelques km de la plage de ponte), l'utilisation des profondeurs (généralement 0-22 m), et la relation positive entre profondeur et durée des plongées en forme de U sur le fond de la mer ont été confirmés.

Des estimations de vitesse de nage fournies par une seule tortue ont confirmé le rôle de repos des plongées en forme de U sur le fond de la mer, pendant lesquelles les tortues ont une flottabilité neutre. Ces plongées permettent de minimiser le temps passé à la surface de l'eau, et donc de minimiser les attaques par des prédateurs de surface. Les profondeurs de repos étant très rarement plus profondes que 19 m, ceci a apporté du soutien à l'hypothèse comme quoi 19 m est la profondeur maximale à laquelle les tortues Vertes d'Ascension puissent avoir une flottabilité neutre. Comme, pour cette espèce, les profondeurs des plongées de repos sont très liées à la taille des réserves d'oxygène, les volumes pulmonaires ont été modélisés afin d'estimer les durées limites de plongée aérobique (Aerobic Dive Limit, ADL) pour des tortues se reposant à des profondeurs différentes. Les résultats suggèrent que les tortues approchent rarement leurs limites physiologiques pendant leurs plongées de repos.

CHAPITRE 4: *A quelle profondeur les tortues Vertes juste écloses nagent-elles ?*

Un animal qui nage près d'un interface air-eau peut engendrer la formation de vagues à la surface de l'eau, et le coût énergétique lié à la création et propagation de ces vagues à la surface de l'eau augmente le coût énergétique de déplacement. On peut prédire que les grands vertébrés marins vont tenter de minimiser les forces de friction liées à ce phénomène, car une telle adaptation comportementale serait très susceptible de les aider à réduire le coût énergétique de nager des distances étendues. En théorie, ceci peut être accompli si les animaux nagent à une distance d'eau moins 2.5-3 fois l'épaisseur de leur corps sous la surface de l'eau.

Parce que les données publiées sur les profondeurs de nage sont plutôt limitées, les profondeurs de plus de 600 plongées de nage pure effectuées par 47 tortues Vertes juste écloses ont été mesurées par observation directe. Les tortues Vertes observées ont eu tendance à nager à peu près à 7 cm sous la surface de l'eau, ce qui était équivalent à environ 3.5 fois l'épaisseur de leur corps. Cette adaptation comportementale est susceptible d'augmenter leur chance de survie, en leur permettant d'augmenter, au maximum, la distance nagée loin des eaux côtières pleines de prédateurs, bien avant que leurs réserves d'énergie ne soient totalement épuisées.

CHAPITRE 5: *La distribution temporelle des tortues Luth (Dermochelys coriacea) dans le Golfe de Gascogne (1979-2000).*

Des informations concernant la distribution temporelle saisonnière de tortues Luth dans le Golfe de Gascogne sont présentées pour une période allant de 1979 à 2000. Au total, 1249 observations de tortues Luth (vivantes ou mortes) sur la côte Atlantique française ont été compilées, à partir de sources publiées dans la littérature scientifique. Les incidences annuelles de tortues vivantes ou mortes étaient plutôt basses de 1979 jusqu'au milieu des années 1990, tandis qu'elles étaient relativement plus élevées après. Les incidences annuelles de tortues vivantes observées en mer ont montré une relation positive avec les incidences annuelles de tortues mortes échouées sur les plages. Pour la période 1979-2000, les observations de tortues mortes ou vivantes présentaient des distributions saisonnières très marquées, bien que les observations de tortues mortes aient eu tendance à culminer plus tard (octobre) que les observations de tortues vivantes (août), et bien que les tortues mortes aient été observées pendant presque tous les mois de l'année (les tortues vivantes étaient surtout observées de juin à octobre).

Les observations de tortues vivantes culminaient, année après année, pendant les mois de plus hautes températures de surface de la mer, et 85% des observations de tortues vivantes étaient faites lorsque ces températures de surface étaient au moins à 18°C. Des changement phénologiques dans les distributions temporelles des tortues Luth n'ont pas été mis en évidence, probablement à cause de la mauvaise résolution de la base de données. Les résultats ont suggéré que des facteurs écologiques et physiques, comme la présence/absence de nourriture et les températures de surface de l'eau, sont probablement des facteurs majeurs dans la détermination des distributions saisonnières de tortues Luth dans les eaux tempérées.

CHAPTER 1

Mid-water diving by experimentally displaced Green turtles

INTRODUCTION

Large marine vertebrates spend most, if not all, their lives at sea, which makes them difficult to study using traditional, land-based methods (Fedak *et al.* 2002). The advent of small devices, such as light/pressure/temperature/heart-rate loggers, or activity/speed sensors has, however, shed light on the formerly rather mysterious lives of these animals in their natural environment. The behavioural and environmental information obtained from such instrumentation has been used to study, for instance, the relationships between diving capabilities and body sizes across species (Schreer 1997), or to research various aspects of swimming or diving physiology (e.g. see a review by Butler & Jones 1997). Time-depth information, although restricted to these two dimensions, allows great insights into the underwater lives of marine animals. Dive profiles (and their possible functions) have been described and classified (e.g. Schreer & Testa 1995), various aspects of diving behaviour (e.g. foraging tactics and strategies[1]) have been modelled and/or tested (e.g. Boyd *et al.* 1995, Carbone & Houston 1996, Thompson & Fedak 2001), whilst the behavioural and physiological implications of diving have been reviewed for a wide range of marine species (Butler & Jones 1997; Hooker & Baird 2001).

Although depth information can be obtained remotely, for instance *via* satellite telemetry, this information must generally be processed or summarised on-board (i.e. before transmission), so as to be sufficiently small to fit within the limitations of, for example, the Argos location system (Fedak *et al.* 2002). As a result of data compression, undetermined amounts of information may be lost, which can undermine the strength and accuracy of the subsequent data interpretation (Burns & Castellini 1998). To circumvent this problem, scientists have traditionally preferred deploying instruments that provide high-resolution depth data (i.e. raw data), even if this procedure may require the capture of the animal for attaching and subsequently retrieving any recording devices (alternatively, a buoyancy mechanism and VHS transmitter to locate the tag may be used; Hooker & Baird 2001). Marine animals that come on-shore to rest, mate or nest, provide great opportunities for the attachment and subsequent retrieval of instruments (e.g. seals; Le Boeuf *et al.* 1986). This is particularly

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[1] Some authors prefer to use the word ‘strategy’ (genetically based decision rules) to predict what an animal will do when competing for a scarce resource, and the word ‘tactic’ for the behavioural components used to pursue a strategy (Krebs & Davies 1993).

pertinent for marine turtles, which nest on sandy beaches, several times per nesting season.

The diving behaviour of several species of marine turtles during the nesting season, or at foraging sites, has been widely studied using Time-Depth-Recorders (e.g. Eckert & Eckert 1989, van Dam & Diez 1997, Houghton *et al.* 2002). In contrast, uncompressed diving information (i.e. this is different from submergence information derived from dive duration) for marine turtles travelling long-distances in the open ocean is scarce (but see e.g. Godley *et al.* 2002c), as a result of obvious logistical obstacles. The population of Green turtles, which breeds and nests at Ascension Island (December-June, Mortimer & Carr 1987), is a typical example of such a disparity of knowledge, since studies on its diving behaviour during the inter-nesting period have predominated in the past (Carr & Coleman 1974, Mortimer & Portier 1989, Hays *et al.* 2000a). In comparison, apart from the submergence or compressed depth information obtained from satellite transmitters (e.g. Hays *et al.* 1999), not much has been known hitherto about the diving behaviour of these turtles when they travel the relatively long-distances from their feeding grounds off the coast of Brazil to Ascension Island, and back.

Many animals travel long distances between their breeding and foraging grounds. As these migrations are energetically costly, one might expect strong selection for adaptations to cope with these journeys (Hedenstrom *et al.* 2002). Green turtles from Ascension Island provide a classical example of such long-distance migrants. During the round trip from Brazil (> 4400 km) and when at Ascension Island, during which time they lay several clutches of eggs (on average three clutches, Mortimer & Carr 1987), Green turtles are thought not to feed, but instead rely on limited energy reserves. Inter-nesting turtles at Ascension Island spend up to 65% of their time resting on the seabed (Hays *et al.* 2000a), presumably so as to minimise their overall energy expenditure. Similarly, one might expect that the physiological constraint imposed by having limited energy reserves will influence their swimming and diving activity during long-distance travel, since the optimisation of performance during these activities will increase chances of survival (Hays *et al.* 1999).

In order to study the navigational mechanisms employed by Green turtles to find Ascension Island, Luschi *et al.* (2001) experimentally displaced (up to 270 km away from the island) five Green turtles that had nested on the island, and tracked their movements *via* satellite telemetry. Advantage was taken of this unique opportunity by attaching high-resolution Time-Depth-Recorders to the displaced turtles, in order to record their diving behaviour as they found their way back to Ascension Island. The present study focused on two types of mid-water dives performed during the homing journeys, since these two types of dives appeared to represent considerable proportions of the time budget of the displaced turtles. Although these reptile-specific dives (i.e. they have been described for the Sea snake, *Pelamis platutus:* Graham *et al.* 1975 & 1987, Rubinoff *et al.* 1986) have previously been described for several species of sea turtles (e.g. Hochscheid *et al.* 1999, Hays *et al.* 2001a, Houghton *et al.* 2002, Minamikawa *et al.* 1997 & 2000), their actual functions remain enigmatic. Possible functions include activities such as resting at depth (Minamikawa *et al.* 1997), surface and hence predator avoidance (Hays *et al.* 2001a), searching (e.g. for cues for locating the island), or even energy-saving swimming (Hochscheid *et al.* 1999). One would predict that if the function of these mid-water dives was to rest, then these dives should predominate at night because of the intrinsic diurnal activity cycle in this species. Also, the horizontal speed of travel would be predicted to decline when more of these dives are performed. If the function of these dives was searching, then this should be apparent in their temporal occurrence during the homing trips, i.e. with changes in temporal occurrence at crucial times of the homing trips (e.g. start and/or end of the homing trips). The discrimination between the two types of mid-water dives was based on one parameter of their shape (the presence/absence of a deeper excursion during descent at depth), whilst differences in dive duration, dive depth and temporal occurrences may equally reflect differences in actual functions. Finally, the existence of a positive relationship between dive durations and dive intervals were also investigated, since this is predicted to shed light on the aerobic/anaerobic nature of these dives.

MATERIALS & METHODS

Fieldwork

Time-Depth-Recorders (LTD_100, depth range 0-100m, LOTEK Marine Technologies, St. John’s, Newfoundland) were attached on Ascension Island (7°57’S, 14°22’W) to the carapaces of five adult Green turtles (turtles A, B, C, D & E), using quick-setting epoxy resin (Foilfast, SFS Components, Cheltenham, U.K.). Satellite transmitters (model ST-18; Telonics Inc., Mesa, Arizona) were also attached to the turtle’s heads using epoxy resin. Turtles were only approached when nesting had finished, in order to minimise disturbance. The individuals were then displaced, by ship, between 60 and 270 km away from the island (these displacements are more thoroughly described in Luschi *et al.* 2001). All devices were removed when turtles returned to re-nest.

Diving information

The ‘homing trip duration’ was defined as the period of time between the moment the turtle was released and its arrival at the Ascension (hence the temporal position of an individual during its homing trip could be calculated as a percentage of the homing trip duration). The time when turtles reached Ascension Island was identified, in the dive record, by the presence of the first flat-bottomed dive to the seabed (these dives are described in Hays *et al.* 2000). The raw depth data (measured every 12 seconds to a resolution of 4 cm) were analysed (Hays *et al.* 2001a) using bespoke software (MultiTrace, Jensen Software Systems, Laboe, Germany) and then Minitab. Mid-water diving encompassed all the movements for which maximum depths were deeper than 5 m. Night-time was defined as 18:00-06:00 GMT, whilst day-time was 06:00-18:00 GMT. These time periods consisted of > 90% darkness or daylight respectively (light levels were determined using Telonics Real-Time Satellite Display, Telonics Inc., Mesa, Arizona, USA).

The proportion of time spent performing mid-water dives during the homing trips was calculated as the ratio of the sum of the durations (in hours) of all the mid-water dives divided by the total duration of the homing trip (in hours). The vertical rate of movement (V, in m s^{-1}) during one sampling interval was defined as the ratio of the vertical distance between two successive depth readings to the length of the sampling interval (i.e. 12 seconds): V = (depth [n+1] – depth [n]) / 12. In this chapter, only the rates of vertical movement during the gradual ascent phase were investigated. These rates were selected as ranging from –0.1 to +0.1 m s^{-1}). The vertical rates of movement during the descent and ascent phases are thoroughly investigated in chapter 2 (pp. 69-91), in relation to changes in depth and buoyancy.

Location information

The positions of the satellite-tracked turtles were obtained *via* the Argos location system (Argos 1989, Argos 1996). In short, the transmitter that is deployed on a sea turtle sends uplinks (radio signals) to polar-orbiting NOAA satellites. The location of the transmitter is then calculated by Argos from the Doppler shift in the frequency of transmissions received by a satellite as it approaches and then moves away from the transmitter on a single overpass. Each location is assigned a level of accuracy, or location class (LC) designated as LC 3, 2, 1, 0, A or B. Of these, LC 3, 2, 1 and 0 may be provided only if at least four uplinks are received on an overpass; LC A and B occur when a location is determined from three and two uplinks respectively. Argos states that the estimated accuracy in latitude and longitude is < 150 m for LC 3, between 150 m and 350 m for LC 2, and between 350 m and 1000 m for LC 1 (the accuracy for LC 0, A and B are much poorer).

Satellite locations were selected and analysed as described in Luschi *et al.* (2001). Briefly, the routes followed by the turtles were reconstructed disregarding those fixes which were considered erroneous, either because they inferred a swimming speed exceeding the biological threshold of 5 km/h or because they were on land. Then, the bee-line distances between selected satellite locations and Ascension Island were calculated using a standard great circle equation (see Luschi *et al.* 1998). These bee-lines distances were used as a proxies of the positions of the turtles relative to the island.

However, in order to relate aspects of diving to the corresponding speed of travel, a finer-scale selection of satellite locations had to be performed, in order to obtain more trustworthy speed values (and hence minimise the relative inaccuracy of the Argos location system). For this purpose, all location classes 1, 2 & 3 were kept, whilst locations of class 0 were discarded (they have the lowest accuracy, Hays *et al.* 2001b). For the remaining location classes (A & B), these locations were kept only if they satisfied two conditions: firstly, being situated less than 10 km apart, and then secondly, being within a time frame of two hours (this is equivalent to an inferred speed of travel of less than 5 km/h). Speed values for pairs of locations more than 12 hours apart were ignored.

RESULTS

During the homing journeys, from the release sites back to Ascension Island, turtles performed mid-water dives, classed as type 1 and type 2 dives (figure 1-1, p. 40, see comprehensive description in Hays *et al.* 2001a). The discrimination between type 1 and type 2 dives was based on the length of the deeper excursion relative to the maximum depth of the dive. Some 'other' mid-water dives, whose shapes presented extreme variability, were also performed.

Aspects of the homing journeys to Ascension Island

The homing journeys of the five individuals lasted between 3.8 and 11.8 days, with turtles having been released between about 60 km and 270 km from Ascension Island (table 1-1, p. 40; see Luschi *et al.* 2001 for a complete description of the displacement experiments and homing routes). Individual turtles performed between 100 and 231 mid-water dives during their respective homing journeys, with mean daily dive numbers ranging from 18.0 to 26.3 mid-water dives (table 1-2, p. 40, presents the respective numbers of mid-water dives performed: type 1, type 2 and 'other' mid-water dives).

Mid-water dives were a significant component of the time budgets: their associated submergences accounted for 29.0 to 50.6% of the homing journey durations (table 1-2, p. 40). Turtles spent up to 114 min over two-hour intervals (e.g. 95.1%, turtle B) performing mid-water dives (figure 1-2 A-E, pp. 41-42). The remaining time was assumed to have been allocated to activities such as breathing at the surface and performing relatively shallower and shorter dives, e.g. travelling dives (Hays *et al.* 2001a). Type 1 and 2 dives represented a major part of the mid-water diving activity for all turtles, since the 'other' (i.e. not type 1 nor type 2) mid-water dives comparatively accounted for less than 10% of all such activity.

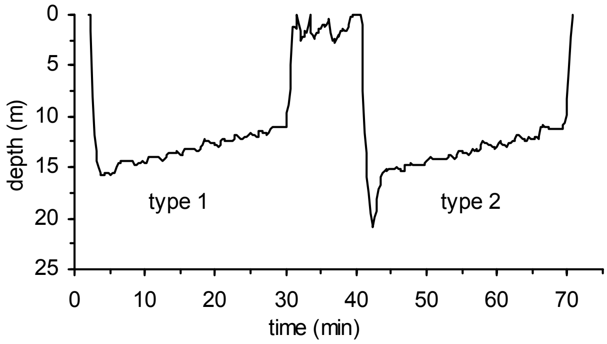


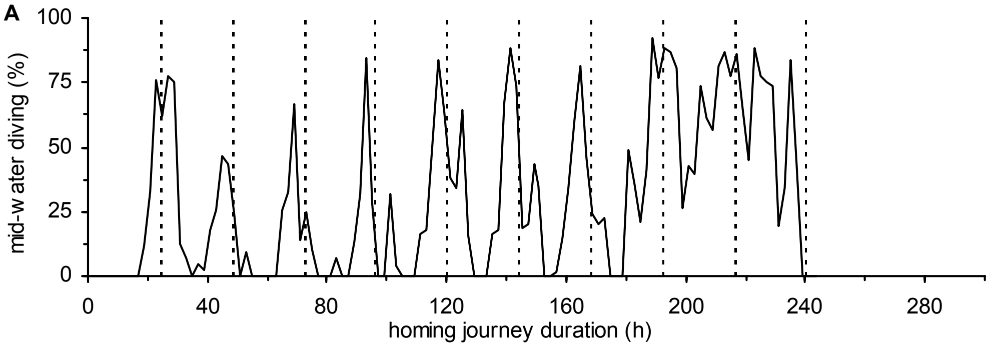
Figure 1-1. Typical examples from turtle C of type 1 (left) and type 2 (right) mid-water dives. At this location, the sea floor is at a depth > 400 m.

Turtle ID	Release date	Bee-line RS-AI (km)	Homing trip hours (days)
A	21/12/99	203.0	244.1 (10.1)
B	21/12/99	203.2	284.9 (11.8)
C	21/12/99	269.9	179.0 (7.4)
D	21/02/00	61.1	93.2 (3.8)
E	22/02/00	64.9	146.5 (6.1)

Table 1-1. General information on the displacements (see also Luschi *et al.* 2001). RS: release site, AI: Ascension Island.

Turtle	Type 1	Type 2	Other mid-water dives	Mean number dives, day^{-1}	Proportion of trip duration, %
A	164	15	12	18.9	31.0
B	106	86	39	19.5	29.0
C	167	13	13	26.0	47.0
D	71	21	8	26.3	50.6
E	57	47	6	18.0	30.3

Table 1-2. Frequencies of type 1, type 2 and other mid-water dives (mean number of dives per day), and the respective proportions of time spent performing these mid-water dives during the homing journeys.


A
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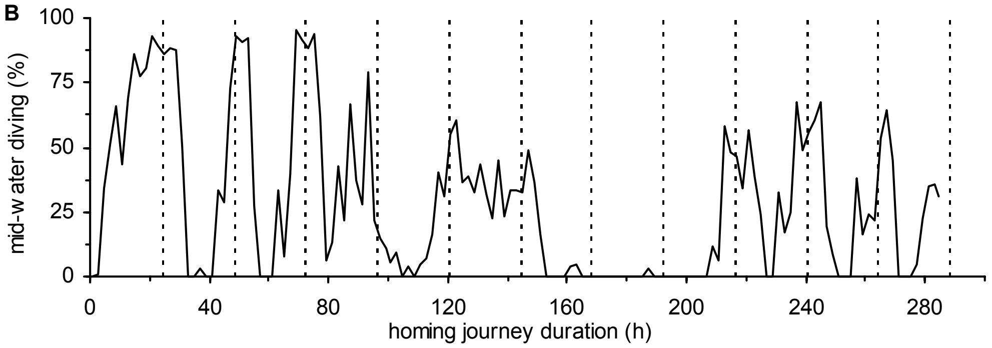
75
50
25
0
mid-water diving (%)
0
40
80
120
160
200
240
280
homing journey duration (h)


B
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75
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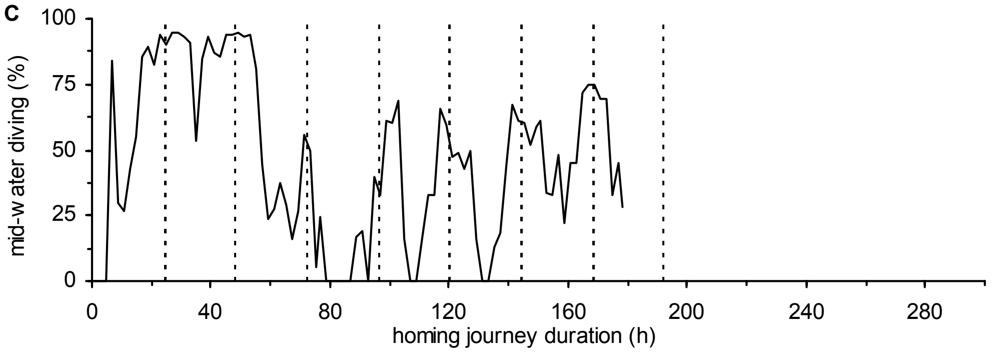
mid-water diving (%)
0
40
80
120
160
200
240
280
homing journey duration (h)


C
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mid-water diving (%)
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40
80
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200
240
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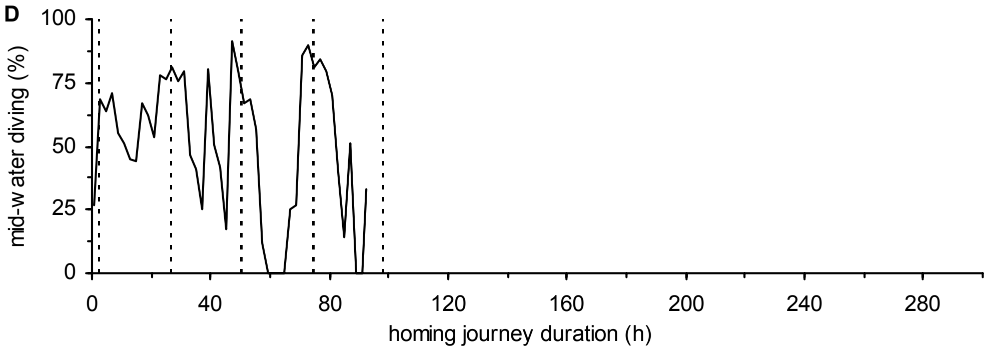
homing journey duration (h)


D
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mid-water diving (%)
0
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80
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homing journey duration (h)

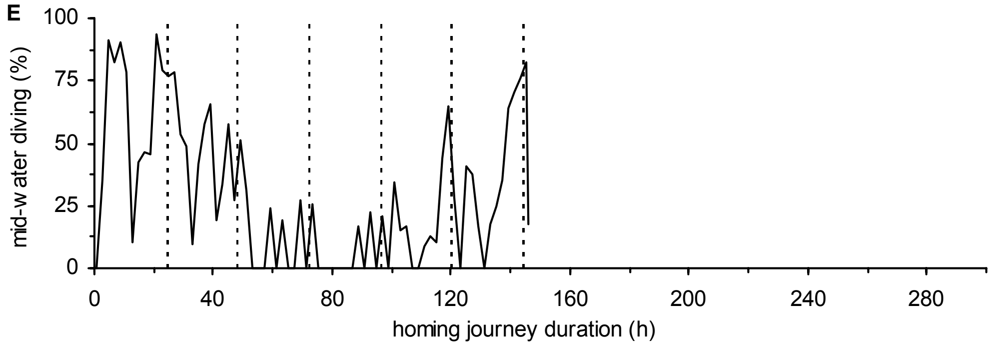


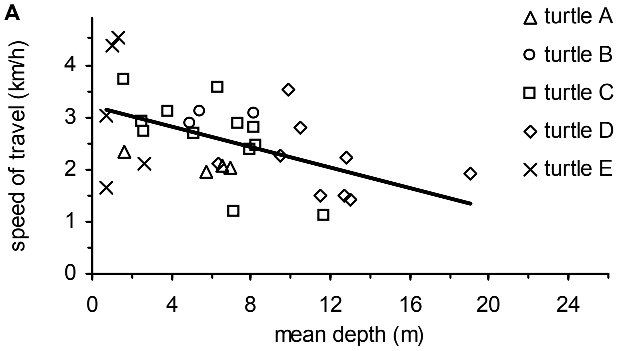
Figure 1-2. Submergence behaviour (as a percentage over two hour periods) resulting from mid-water diving (type 1 & 2 dives, and any other mid-water dives), during the homing journeys. A, B, C, D & E are for turtles A to E, respectively. The dotted vertical lines show midnight.

Speed of travel and mid-water diving behaviour

For each turtle investigated individually, there were too few accurate speed values (i.e. values that would be calculated from locations of adequate accuracies) to perform statistical tests. Since no large difference in speed between individuals was detected, the speed data for the five individuals was combined. In such an analysis, the speed of travel significantly declined when the mean of all the depth readings (at 12 second intervals) during the period of time between the two satellite locations increased (figure 1-3 A, p. 44, regression analysis, data of five individuals, $F_{0.05,\,1,\,32} = 10.55$, $p = 0.002$, $r^2 = 0.25$). This suggested a relationship between diving behaviour and speed of travel. Predictably, these same mean depth values were negatively related with the corresponding proportions of time spent performing type 1 & 2 dives (regression analysis, data of five individuals, $F_{0.05,\,1,\,32} = 61.66$, $p < 0.0001$, $r^2 = 0.66$). Finally, the speed of travel significantly declined when the corresponding proportions of time spent performing type 1 & 2 dives increased (figure 1-3 B, p. 44, regression analysis, data of five individuals, $F_{0.05,\,1,\,32} = 6.16$, $p = 0.018$, $r^2 = 0.16$), which confirmed the existence of a negative link between mid-water diving activity and speed of travel.

Relationships between depth, duration and vertical rate

Mean vertical rates of movement during the gradual ascent phase ranged from 4.4×10^{-03} m s^{-1} (SD = 2.0×10^{-03} m s^{-1}, $N = 179$ type 1 & 2 dives, turtle A) to 9.3×10^{-03} m s^{-1} (SD = 7.4×10^{-03} m s^{-1}, $N = 192$ type 1 & 2 dives, turtle B). For type 1 & 2 dives, mean depth, duration and the mean rate of vertical movement during the gradual ascent phase were found to be closely interlinked with each other. For all five individuals, deeper type 1 & 2 dives tended to be shorter (figure 1-4, p. 45, regression analyses). Similarly, type 1 & 2 dives tended to be shorter when the mean rates of vertical movement during the gradual ascent phase were faster (regression analyses; (A): $F_{0.05,\,1,\,178} = 47.4$, $p < 0.001$, $r^2 = 0.21$; (B): $F_{0.05,\,1,\,191} = 161.7$, $p < 0.001$, $r^2 = 0.46$; (C): $F_{0.05,\,1,\,179} = 130.4$, $p = 0.011$, $r^2 = 0.42$; (D): $F_{0.05,\,1,\,91} = 131.4$, $p < 0.001$, $r^2 = 0.59$; (E): $F_{0.05,\,1,\,103} = 68.1$, $p < 0.001$, $r^2 = 0.40$). Finally, deeper type 1 & 2 dives tended to show faster mean vertical rates of movement during the gradual ascent phase (regression analyses; (A): $F_{0.05,\,1,\,178} = 83.5$, $p < 0.001$, $r^2 = 0.32$; (B): $F_{0.05,\,1,\,191} = 38.8$, $p < 0.001$, $r^2 = 0.16$;



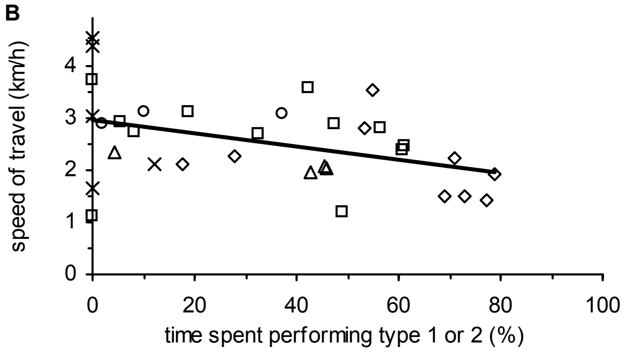


Figure 1-3. (A) The relationship between speed of travel (as calculated from selected satellite locations) and the mean of all the depth readings during the interval of time between the two successive satellite locations used to estimate the speed of travel (speed of travel = - 0.096 x mean depth + 3.192). (B) The relationship between speed of travel and the proportion of time spent performing type 1 & 2 dives during the same interval of time (speed of travel = - 0.012 x proportion of time + 2.957). The regression lines consider data points from all five turtles.

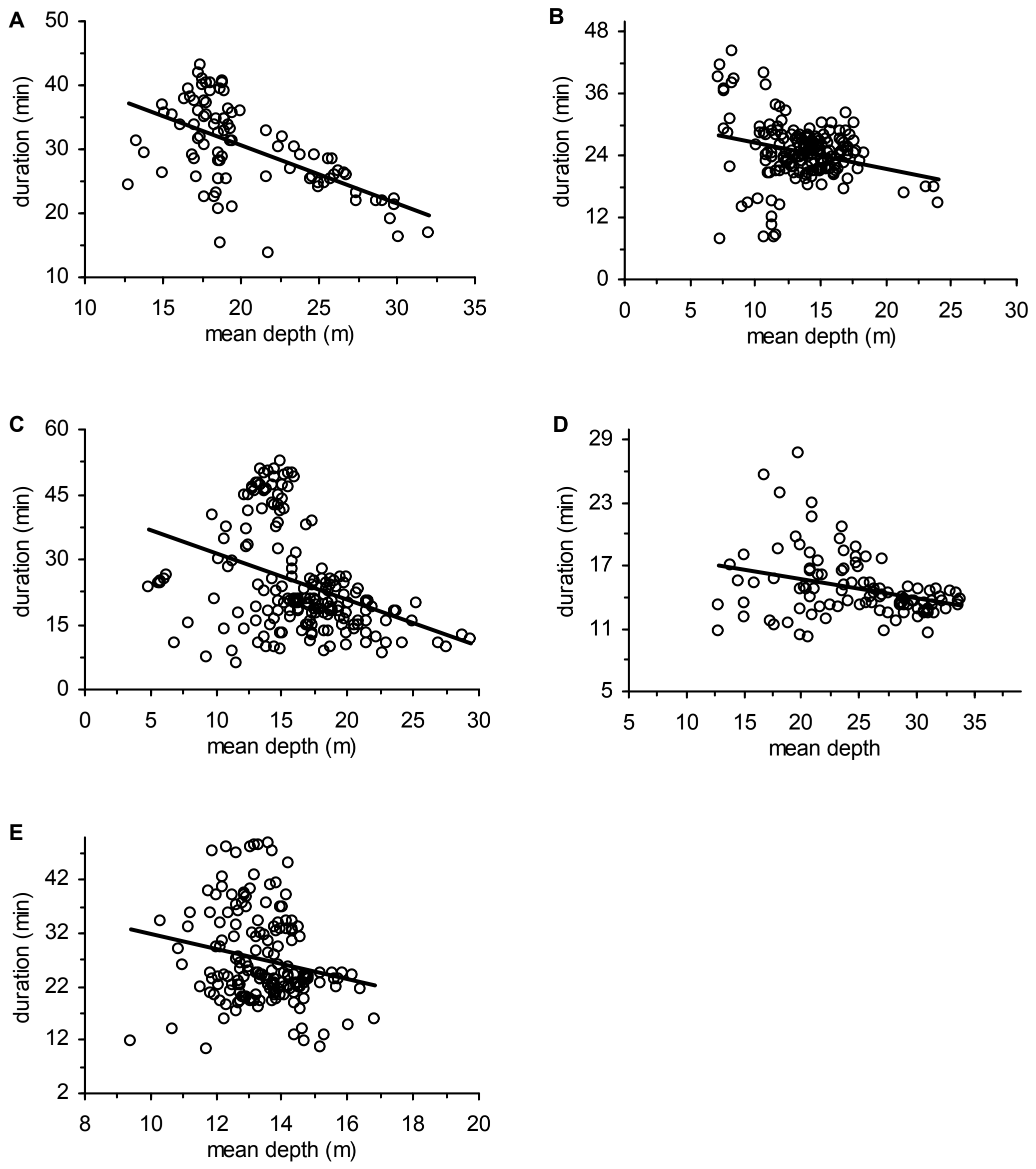


Figure 1-4. Relationships between duration and mean depth for type 1 & 2 dives. A, B, C, D & E are for turtles A-E, respectively. (A): $F_{0.05,\,1,\,178} = 11.6$, $p < 0.001$, $r^2 = 0.06$; (B): $F_{0.05,\,1,\,191} = 29.7$, $p < 0.001$, $r^2 = 0.13$; (C): $F_{0.05,\,1,\,179} = 6.5$, $p = 0.011$, $r^2 = 0.03$; (D): $F_{0.05,\,1,\,91} = 46.1$, $p < 0.001$, $r^2 = 0.34$; (E): $F_{0.05,\,1,\,103} = 11.0$, $p < 0.001$, $r^2 = 0.01$.

(C): $F_{0.05, 1, 179} = 60.1$, $p = 0.011$, $r^2 = 0.25$; (D): $F_{0.05, 1, 91} = 202.8$, $p < 0.001$, $r^2 = 0.69$; (E): $F_{0.05, 1, 103} = 91.6$, $p < 0.001$, $r^2 = 0.47$).

The different portions of the homing trips

The durations and mean depths of type 1 or type 2 dives were quite variable throughout the homing journeys. Dive durations and mean dive depths were averaged for fixed temporal portions of the homing journeys (here for each 5% of each journey duration). These averaged durations tended to shorten (figure 1-5 A-E, p. 47) while the averaged mean depths tended to be deeper (figure 1-6 A-E, p. 48) towards the end of the journeys, despite some degree of inter-individual variability (turtle A for duration and turtle C for depth). This relative temporal change in diving behaviour tended to coincide with the final, island-directed legs of each turtle's route (shown in red, figure 1-5 A-E, p. 47, and 1-6 A-E, p. 48). Luschi *et al.* 2001 described these final legs in more detail because they were the directions followed by the turtles to approach the island. The final leg of each turtle's route started at different times during the homing journeys: at 58.4% of the journey duration for turtle C, and between 71 and 78% of the journey durations for the other individuals. This corresponded to the final legs starting at different bee-line distances from the island (range: from about 51 km for turtle D to about 182 km for turtle A).

Turtle B, whose homing track also included a full loop, showed an additional temporal change in diving behaviour. Two portions of its route were of special interest and belong, in part, to the above-mentioned loop: the 'middle' segment was at the start of the loop and the 'final' segment was the final leg of the homing journey (figure 1-7, p. 49). These two segments of the homing journey of turtle B had comparable island-directed orientations and their tracks were spatially close (and they ran parallel each other), separated only by a few kilometres. During both these segments of the homing route of turtle B, averaged durations and averaged mean depths of type 1 and type 2 dives tended to be shorter and deeper than at any other time during the homing journey of that turtle.

Such temporal changes in behaviour between legs of the journeys were tested for significance (although turtle A and turtle C were excluded for testing changes in duration and depth, respectively, because they did not show such temporal changes in

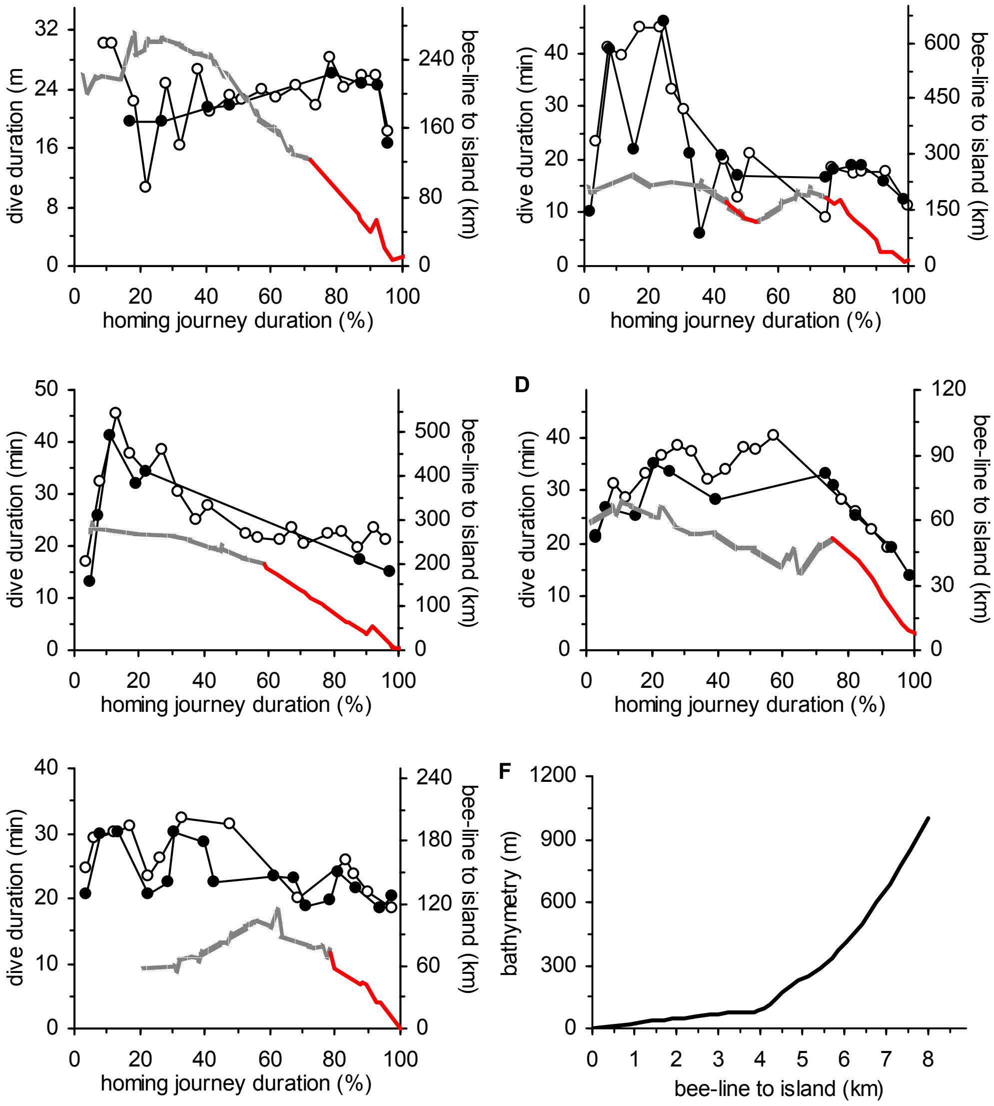


Figure 1-5. (A-E) Primary axis: mean durations for type 1 (o) and type 2 (•) dives, per 5% time intervals during the homing journeys (A, B, C, D & E are for turtles A-E, respectively). Secondary axis: bee-line distance of each satellite location to Ascension Island (grey line; the final, island-directed leg is shown in red). Figure 1-5 B: the ‘middle leg’ of turtle B’s route is shown in red. (F) The bathymetry around Ascension Island, corresponding to the direction of approach (north-east) followed by the five turtles.

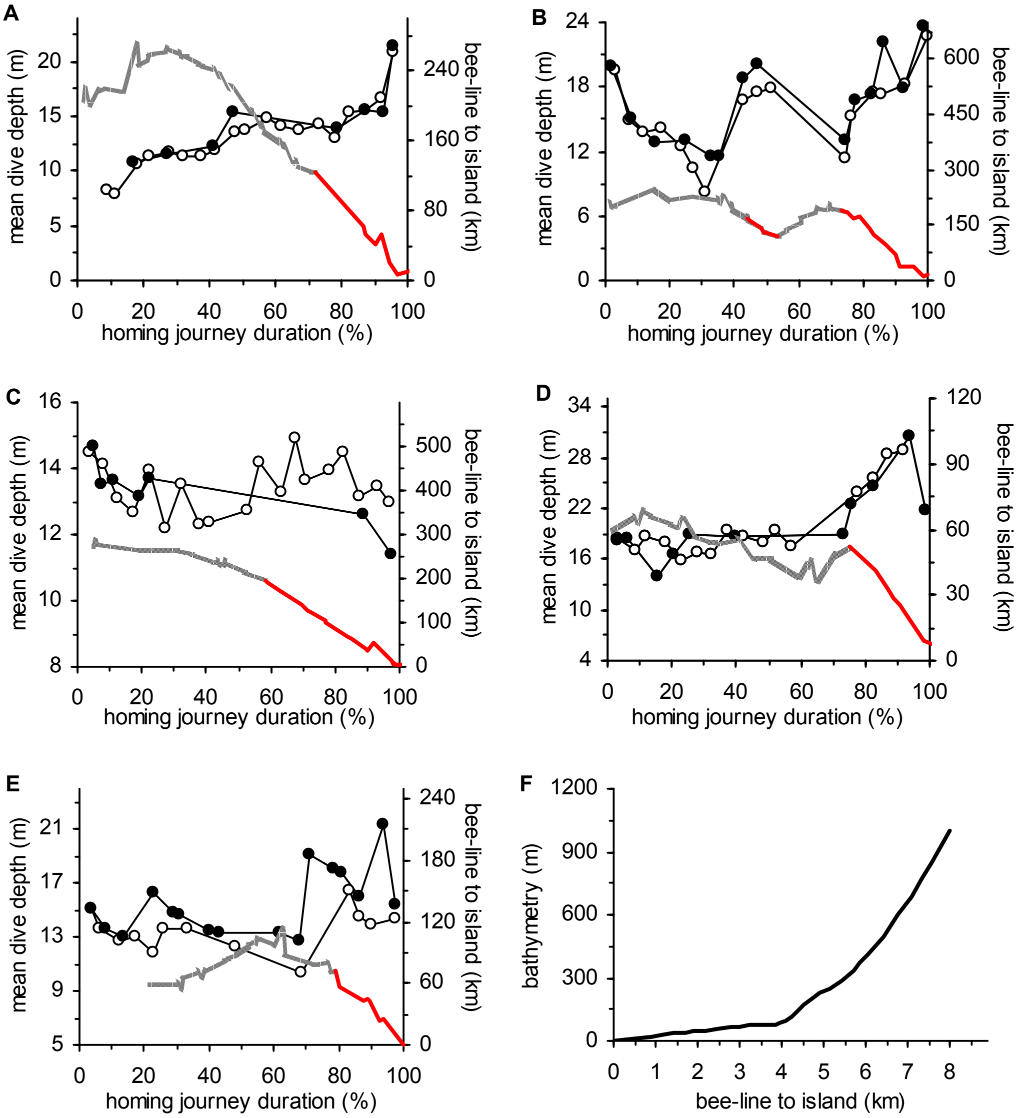


Figure 1-6. (A-E) Primary axis: means of mean depths for type 1 (o) and 2 (•) dives, per 5% time intervals during the homing journeys (A, B, C, D & E are for turtles A-E, respectively). Secondary axis: bee-line distance of each satellite location to Ascension Island. Figure 1-6 B: the ‘middle leg’ of turtle B’s route is shown in red. (F) The bathymetry around Ascension Island, corresponding to the direction of approach (north-east) followed by the five turtles.

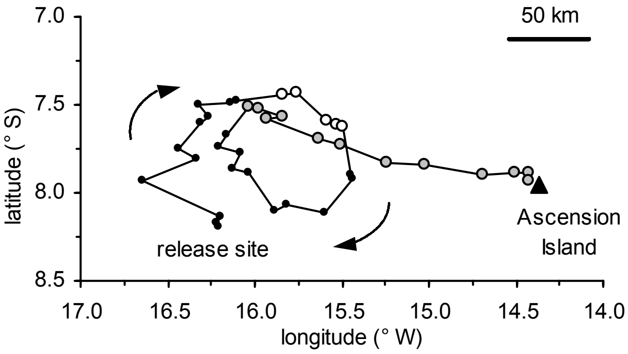


Figure 1-7. The tracks of the homing journey of turtle B (adapted from Luschi *et al.* 2001). The island-directed legs are highlighted ('middle' leg in white, 'final' leg in grey). The 'middle' leg is at 43.8-49.3% of the homing journey duration and the 'final' leg is at 73.3-100%.

behaviour). Type 1 and type 2 dives were significantly shorter during the final legs of the journeys (one-tailed paired t-test, $N = 4$ turtles, type 1: t = 5.1, $p < 0.05$, type 2: t = 3.9, $p < 0.05$), as well as being significantly deeper (one-tailed paired t-test, $N = 4$ turtles, type 1: t = 2.7, $p < 0.05$, type 2: t = 3.9, $p < 0.05$).

The final legs were located in waters deeper than 1000m practically for all their durations (figure 1-5 F, p. 47 and figure 1-6 F, p.48), hence any change in behaviour observed during the final legs were unlikely to be due to direct changes in bathymetry.

Diel patterns of mid-water diving

Mid-water diving activity showed a clear diel pattern (figure 1-2 A-E, p. 42), but most of this pattern was probably due to the very regular temporal occurrence of type 1 dives, since these dives occur principally at night (figure 1-8 A-E, part 1/2, p. 51). In contrast, type 2 dives (as well as the 'other' mid-water dives) tended to be equally distributed during the day and at night (figure 1-8 F-J, part 2/2, p. 52), for all but one individual (turtle B in figure 1-8 G). There was no clear diel pattern for the mean vertical rates of movement for type 1 & 2 dives, although turtles B and D showed some of their fastest rates of vertical movement during the day-time.

Type 1 dives versus type 2 dives

For all but one individual (turtle C), type 1 dives lasted significantly longer than type 2 dives (one-tailed unpaired t-tests; turtle A: t = 2.3, $p = 0.032$, df = 19; turtle B: t = 6.6, $p < 0.0001$, df = 165; turtle D: t = 2.5, $p = 0.016$, df = 37; turtle E: t = 5.6, $p < 0.0001$, df = 98). On average, type 1 dives lasted between 14 and 54% longer than type 2 dives (mean durations for each type of dives are given in Hays *et al.* 2001a). The mean rates of vertical movement during the gradual ascent phases of type 2 dives tended to be faster than the ones during type 1 dives, although this difference was significant only for two turtles (one-tailed unpaired t-tests; turtle B: t = 3.8, $p = 0.0002$, df = 179; turtle E: t = 8.3, $p < 0.0001$, df = 71).

In contrast with the clear diel patterns of type 1 dives throughout the homing journeys, type 2 dives (and the 'other' mid-water dives) tended to occur either at the start, or the end, of the homing journeys, or during both times (figure 1-9 A-E, p. 53). For all but one turtle (turtle C), type 2 dives (and the other mid-water dives) were

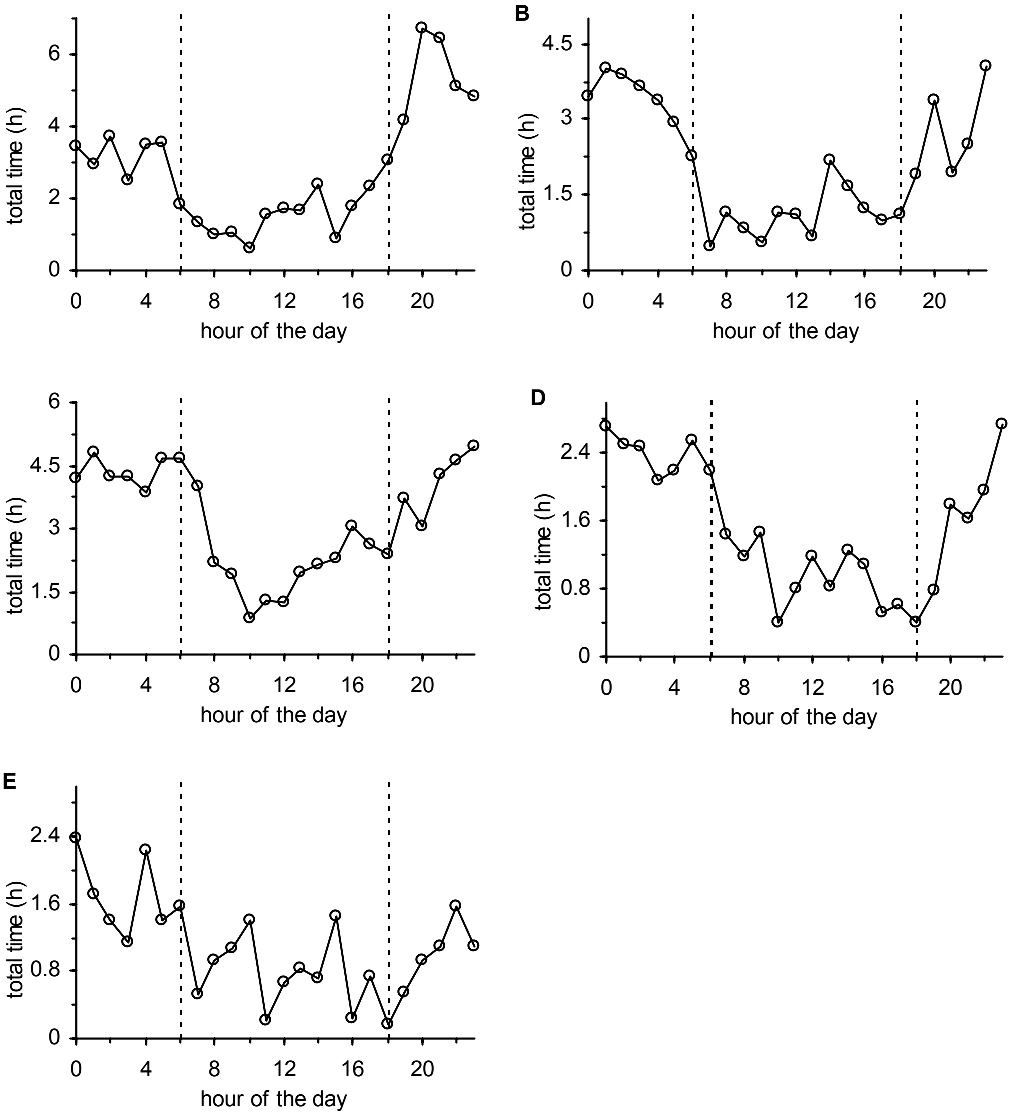


Figure 1-8, part 1/2. (A-E): total time (for each hour of the day) spent performing type 1 dives (o) during the homing journeys (A, B, C, D & E are for turtles A-E, respectively).

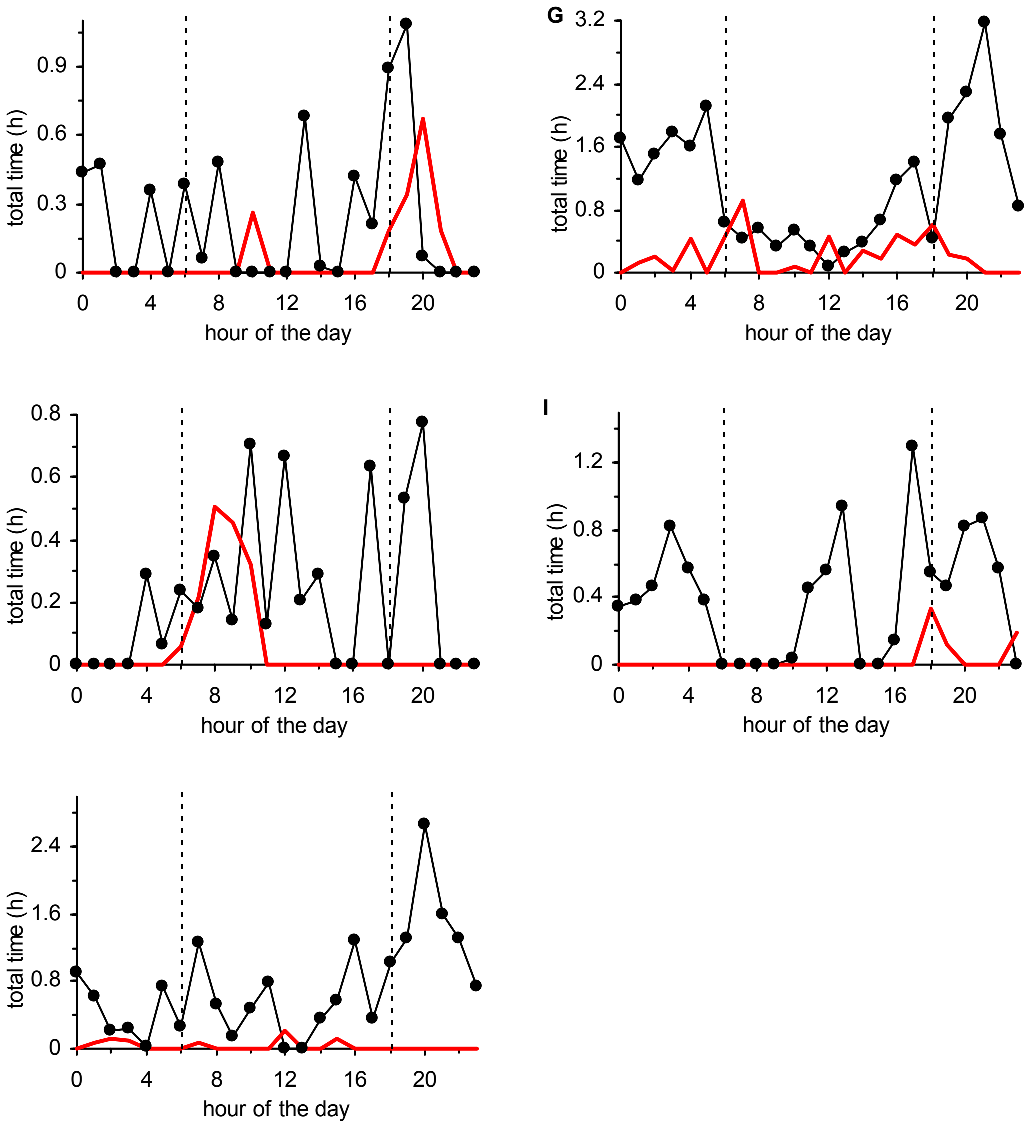


Figure 1-8, part 2/2. (F-J): total time spent performing type 2 dives (•) and the other mid-water dives (red line) during the homing journeys (F, G, H, I & J are for turtles A-E, respectively).

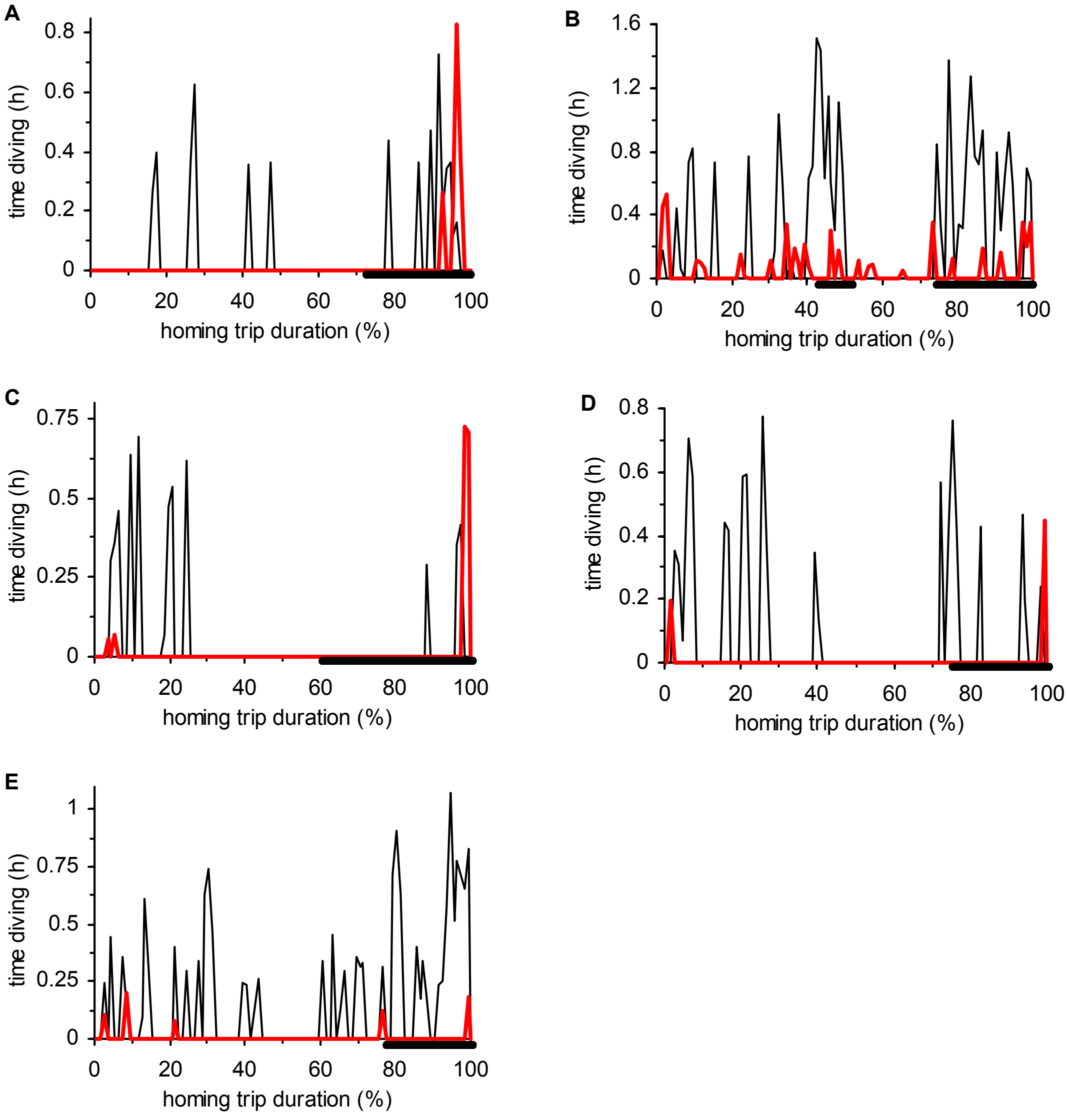


Figure 1-9. Total time spent performing type 2 dives (in dark) and the other mid-water dives (in red), for each 5% time intervals during the homing journeys (A, B, C, D & E are for turtles A-E, respectively). The respective positions of the final, island-directed legs are shown on the x-axis (the middle leg is shown in a similar way for turtle B in figure 1-9 B).

comparatively more frequent during the final, island-directed legs of the return journeys. The considerable discrepancies between the maximum and mean depths of type 2 dives (figure 1-10 A-E, p. 55, solid bars) were probably a consequence of the extremely variable vertical lengths of the deeper excursions during these deep type 2 dives (e.g. figure 1-11, p. 56). In comparison, during type 1 dives, the differences between the maximum and the mean depths were usually more restricted in amplitude (figure 1-10 A-E, p. 55, open bars), because of the absence of the deep excursions before the start of the gradual ascent phase.

Finally, apart from one individual (turtle C), the deepest type 2 dives (up to 7 type 2 dives, depending on the turtle, with maximum depths ranging from 34.8 to 64.2 m) consistently occurred towards the end of the final, island-directed legs, i.e. just before the end of the homing trips. Moreover, turtle B also performed some of its deepest type 2 dives during the middle, island-directed leg of its homing journey. These relatively deep type 2 dives, whether they occurred at the start and/or at the end of the homing journeys (and during the ‘middle leg’ for turtle B) were all associated with relatively fast rates of vertical movement during the gradual ascent phases.

The ‘other’ dives

Apart from one individual (turtle B), the other mid-water dives (i.e. neither type 1 nor 2 dives) followed similar temporal patterns of occurrence as type 2 dives. The deepest of these dives (up to 5 dives for some turtles, dives whose maximum depths ranged from 34.6 to 74 m) occurred towards the end of the final, island-directed legs of the homing journeys, i.e. just before the end of the homing trips. The time when turtles reached Ascension Island was designated as occurring when the first flat-bottomed dive to the seabed was recorded (see Materials & Methods). The first flat-bottomed dives were almost always much deeper (range: 32.6 to 64.8 m) than the more classical U-shaped resting dives that eventually followed (dives to 10-25 m, dives described in Hays *et al.* 2000a). Also, these deep flat-bottomed dives were always preceded by the very deep type 2 dives mentioned above (see for example turtle B shown in figure 1-12, p. 56).

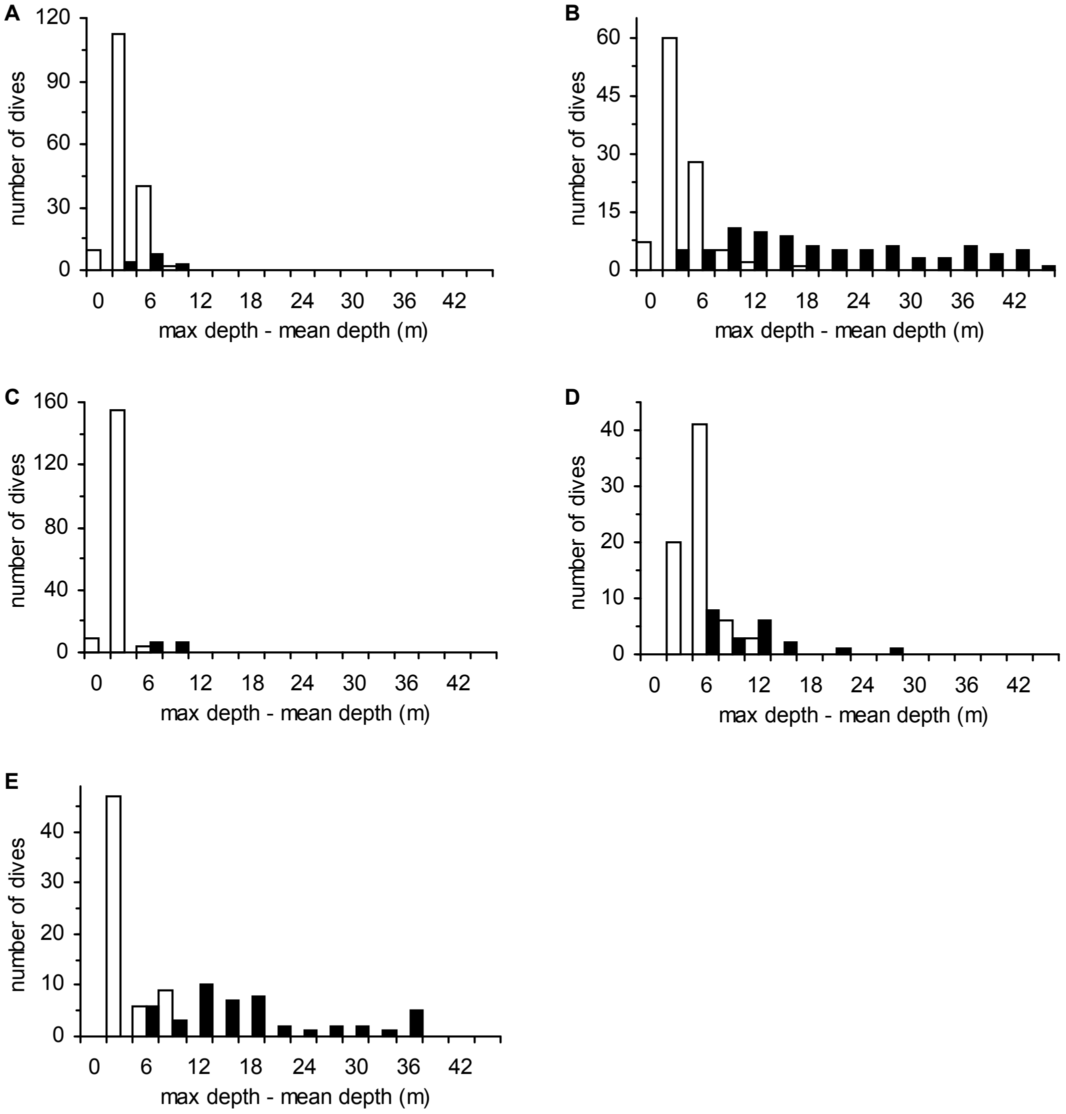


Figure 1-10. Frequency distributions for the differences between the maximum and mean depths for each dive, for type 1 dives (open bars) and type 2 dives (solid bars).

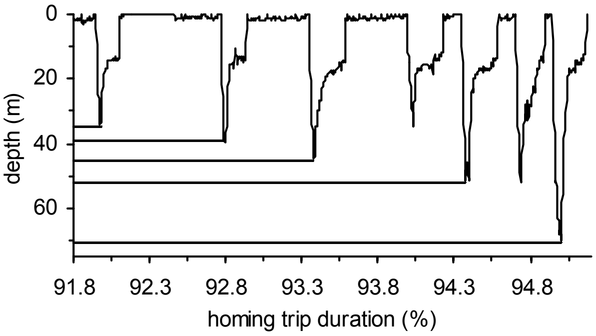


Figure 1-11. A series of type 2 dives showing increasing maximum dive depths, during the final, island-directed leg of turtle E's homing journey.

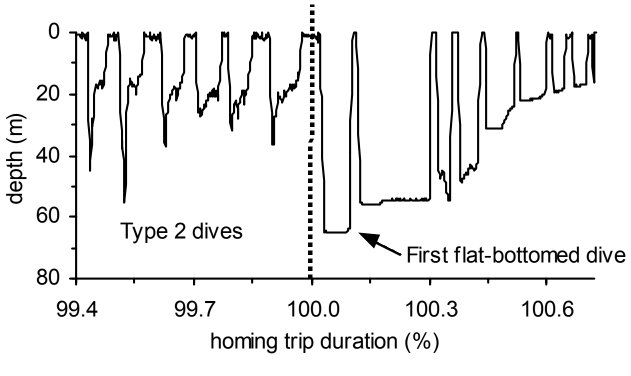


Figure 1-12. A series of type 2 dives followed by the first flat-bottomed dives to the sea bed (turtle B). The dashed line marks the end of the homing trip for this individual.

Bouts of type 1 and 2 dives

Time intervals between type 1 and/or type 2 dives were as short as 48 seconds in duration (turtle E), but most post-dive intervals lasted 20 minutes or less (this proportion ranged between 57 and 70%, depending on the turtle). The values of the dive intervals were highly skewed towards short dive intervals, with modal dive intervals being either 2-4 minutes (turtles C, D & E) or 4-6 minutes (turtles A & B).

With respect to 'bouts' of several type 1 and/or 2 dives (the bouts were obtained by selecting dive intervals of length < 40 min.), turtles usually performed a few short (typically < 5 min.) and shallow (typically < 5 m) dives during the dive intervals (e.g. figure 1-13 A, p. 58). Usually, the twelve-second sampling interval was too coarse to accurately identify these short and shallow dives (e.g. figure 1-13 B & D, p. 58; Hays *et al.* 2001a), but it was usually possible to visually identify some as being travelling dives. The depth distribution and durations of the dive intervals during bouts of dives did not show any obvious diel pattern, and the depth distribution was very similar to the depth distribution of the dive intervals outside dive bouts.

During bouts of type 1 and type 2 dives, turtles spent variable times at or close to the surface (i.e. between 0 and 0.5 m below the surface), in the time intervals between dives (figure 1-13 A-D, p. 58). Turtles spent between 0.9 and 15.0 minutes at or close to the surface, but time spent at or close to the surface during dive intervals ranged between 2.5 and 3.8 minutes. The proportions of time, during the dive intervals, spent at or close to the surface varied, on average, between 34.3 and 46.0% depending on the turtle, but all individuals could spend up to 100% of their dive intervals at or close to the surface (e.g. figure 1-13 C, p. 58).

There was no significant relationship between the post-dive interval and the duration of the type 1 or 2 dive that preceded it (regression analyses, $p > 0.05$ for each turtle). For all but one individual (turtle E), however, the duration of a type 1 and/or 2 dive during a bout increased significantly (regression analyses, $p < 0.01$ for each turtle, r^2 varying from 0.20 to 0.34) with the time spent at or close to the surface during the pre- or post-dive interval. If the data for these four turtles was pooled, type 1 and/or 2 dives lasted significantly longer when the proportion of time spent close to the surface during the pre- or post-dive intervals increased (figure 1-14 A & B, p. 59).

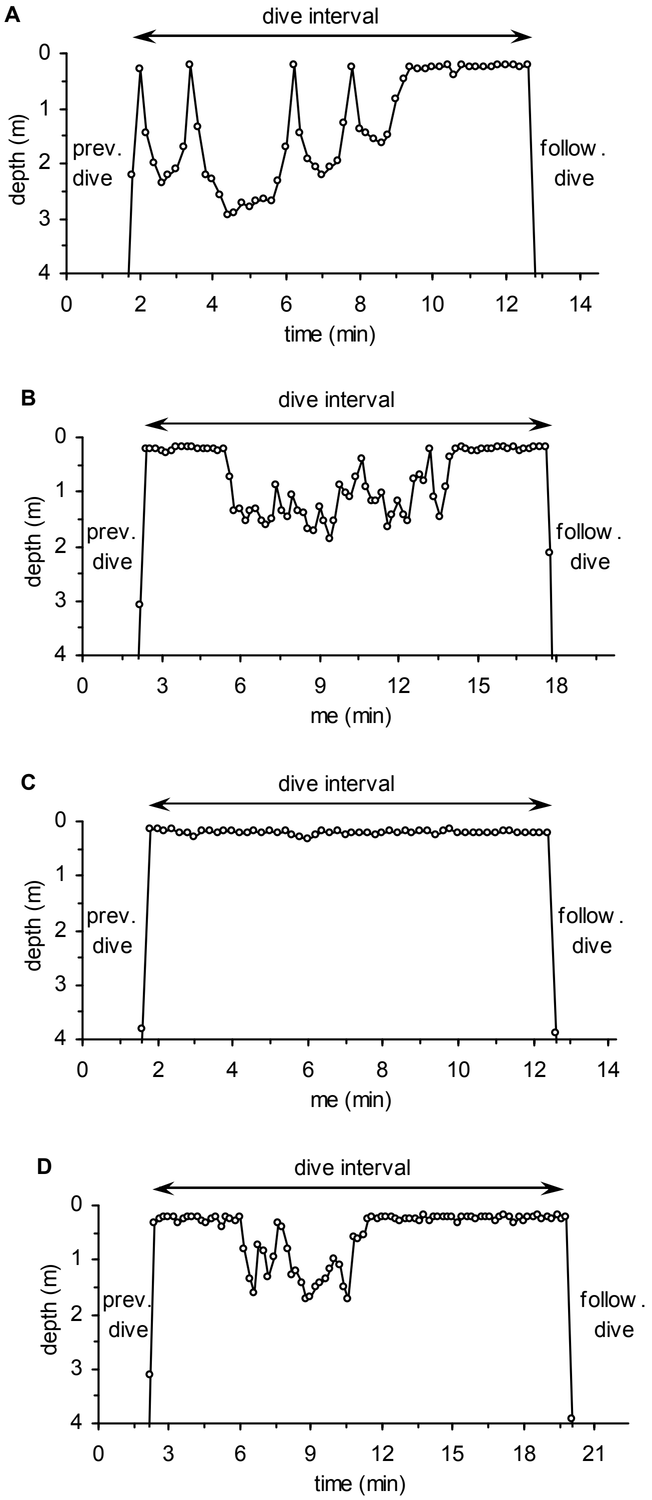


Figure 1-13. Typical examples of the dive intervals during a bout of type 1 and/or 2 dives (figure 1-13 A: turtle D, figure 1-13 B, C & D: turtle B).

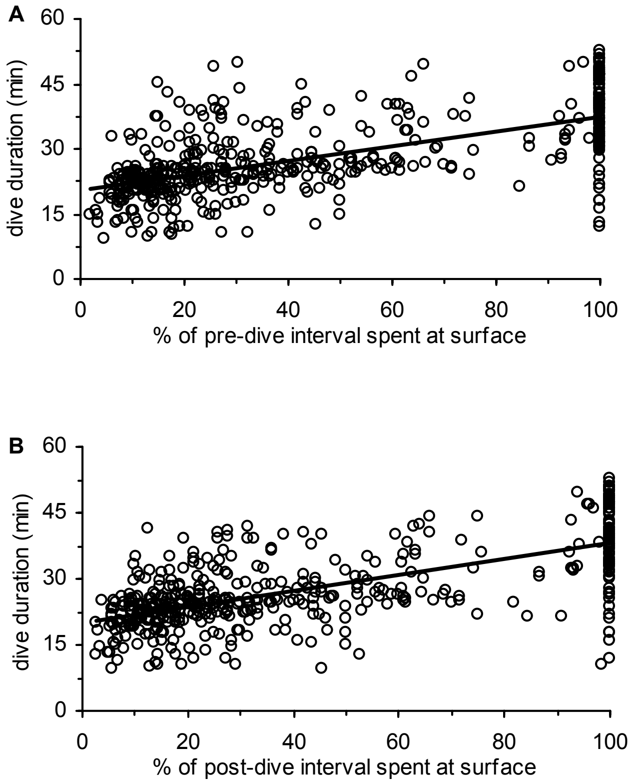


Figure 1-14. Combined data for turtles A, B, C & D showing the relationship between dive duration (type 1 & 2 dives) and the proportion of time during the dive interval spent at the surface (i.e. between -0.5 and 0 m), (A) before the dive ($F_{0.05,\ 1,\ 458} = 219.6$, $p < 0.0001$, $r^2 = 0.39$), and (B) after the dive ($F_{0.05,\ 1,\ 458} = 366.7$, $p < 0.0001$, $r^2 = 0.44$).

DISCUSSION

In the present study, the concomitant use of satellite telemetry and high-resolution depth loggers has provided new insights into the functions of the mid-water dives performed by a shallow diving sea turtle, when it travels in the open ocean. Mid-water diving represented a considerable proportion of the diving activity during the homing trips, and the speed of travel tended to decline when more time was spent mid-water diving. Despite some inter-individual variability, type 1 dives tended to occur mostly at night, whilst type 2 dives preferentially occurred at the start and/ or end of the trips, although both type of dives were probably aerobic and tended to shorten and deepen during the final legs of the trips.

Diving behaviour during the homing journeys

As noted by Hays *et al.* (2001a), it is rather unexpected that turtles do not spend most of their homing journeys performing relatively short and shallow travelling dives (where they would be predicted to be swimming at the speed of minimum cost of transport). Indeed, one may predict that such a behaviour would allow the turtles to reach their homing target in the shortest time possible, hence minimising basal metabolic costs. In contrast, the current study showed that mid-water diving represented a considerable fraction of the diving activity during the homing journeys, accounting for up to 50% of the journey's durations, the rest of the time being allocated to short and shallow travelling dives. Furthermore, mid-water diving clearly slowed the speeds of travel, potentially increasing the overall duration of the homing trips. This indicates that the five displaced turtles had to optimise their behaviour, i.e. find the best compromise among at least two conflicting requirements: the need to minimise trip duration (and basal metabolic costs) and the need to periodically perform these mid-water dives (which then increase travel time).

Luschi *et al.* (2001) hypothesised that during the final, straight, island-directed legs of the homing journeys, turtles may establish sensory contact at variable distances from Ascension Island. This sensory contact was hypothesised to be a wind-borne cue, i.e. possibly auditory or olfactory, since approach mostly occurred from the direction opposite to the trade wind (north-east). Having established contact, turtles would then be able to swim on a direct route to the island. Despite some degree of inter-individual variability, the present study showed that a temporal change in diving behaviour coincided with the turtles entering these final, island-directed legs of their respective homing journeys. It was found that type 1 & 2 dives, for most turtles, tended to (1) be shorter in duration, (2) reach greater depths, and (3) exhibit faster mean rates of vertical movement (during the gradual ascent phases) during the final legs of the journeys, in contrast to the initial portions of the journeys. This change of behaviour cannot be directly attributed to a change of bathymetry at the location of the turtles, since the depth of the sea floor remained predominantly greater than 1000 m.

Additionally, turtle B presented a similar temporal change in diving behaviour (i.e. shorter and deeper type 1 & 2 dives, with relatively fast mean rates of vertical movement during the gradual ascent), a change which coincided with an island-directed leg of its return route (i.e. the 'middle' leg). It remains uncertain whether turtle B actually established sensory contact with the island during this 'middle' island-directed leg and if so, why it subsequently lost it (as shown by the loop formed by the tracks).

In order to find some way of explaining these temporal behavioural changes, it may be useful to consider the physiological processes that may take place when turtles are at depth. Submergence duration is generally linked to activity levels in sea turtles (Hays *et al.* 2000b). Shallow-diving sea turtles (such as the Loggerhead turtle, *Caretta caretta*) and the Green turtle are thought to passively control their buoyancy at depth by proportionately inflating their lungs before submerging (Milsom 1975, Minamikawa *et al.* 1997, 2000, Hays *et al.* 2000a, 2001a). During the bottom phases of U-shaped resting dives to the sea bed and during the gradual ascent of type 1 & 2 dives, sea turtles (such as Green and Loggerhead turtles) are thought to be neutrally buoyant. Minamikawa *et al.* (2000) suggested that the buoyancy during the gradual ascent phase of type 1 & 2 dives may change with time. When at depth, the oxygen present in the lungs would be utilised, whilst the carbon dioxide produced rather than entering the lungs would remain bound in the blood until the dive ends, a phenomenon first described for the Sea snake (Graham *et al.* 1975, 1987). Consequently, lung volume would decrease as the dive progresses and, to counter this gradual reduction in lung volume, the turtles would gradually ascend in the water column, to maintain neutral buoyancy. One may consequently predict that the vertical rate of movement during the gradual ascent phase is a proxy for the rate of oxygen utilisation, i.e. the turtle's metabolic rate during the dive. Greater metabolic rates would be associated with faster rates of vertical movement during the gradual ascent phase, as a result of buoyancy changing faster, due to oxygen stores being more quickly depleted.

Dives of shorter duration (which were usually deeper) tended to be associated with faster mean vertical rates of movement during the gradual ascent phases. This suggests that deeper and shorter dives would have greater rates of energy expenditure when compared to dives of longer duration (which were usually shallower). At Ascension Island, the resting depths (range 15-25 m) appeared a proxy for the lung volume upon leaving the surface (and hence for the amount of oxygen stored in the lungs), since this volume of air would be necessary to achieve neutral buoyancy on the sea bed (Hays *et al.* 2000a). This explains why deeper dives tend to last longer than shallower counterparts where associated lung volume (and hence oxygen store) upon leaving the surface would be smaller. In contrast with U-shaped resting dives to the sea bed, type 1 & 2 dives showed a negative relationship, with deeper dives being of a shorter duration than shallower dives. In contrast, several studies found positive relationships between depth and duration for similar mid-water dives (Minamikawa *et al.* 1997, 2000, Hoschsheid *et al.* 1999). These dives took place, however, during the inter-nesting period, rather than during open-water long-distance travel. The absence of a positive relationship between depth and duration (indeed a negative relationship) in the present study indicates that the primary function of type 1 and 2 dives is not resting *per se*. Dives to deeper depths are probably associated with greater overall energy expenditures, than dives to shallower depths.

Upon release in the ocean, experimentally displaced turtles are likely to be unsure of their position relative to Ascension Island, and of the distance separating them from their homing target. It is possible that they adopt a ‘safe’ (i.e. energy saving) diving behaviour, at least until they can locate the island and assess the length and duration of their homing trip. One may speculate that when sensory contact with the island seems established (supposedly at the start of the final, island-directed legs), turtles would then tend to adopt a ‘less safe’ diving behaviour, involving shorter and deeper type 1 & 2 dives, with faster mean vertical rates of movement during the gradual ascent, hence with potentially greater overall energy expenditures.

The role of type 1 dives

Some marine or aquatic animals may minimise surface time to reduce the probability of attack by surface predators (Elephant seals: Crocker *et al.* 1997, Le Boeuf *et al.* 2000; freshwater turtles, *Rheodytes leukops*: Gordos *et al.* 2003). In effect, when an animal is close to the surface, it is silhouetted against the brighter background from above, resulting in it being more detectable by potential predators from below (Denton 1971). While it is true that the Green turtle possesses a counter-shading adaptation (i.e. a white plastron), which minimises the silhouette effect, type 1 dives (and this can be extended to type 2 dives) might reduce the time spent too close to the surface, since almost all the dive time is spent at depth, gradually ascending in the water column. Hence, type 1 dives (and type 2 dives) may reflect a camouflage behaviour aimed at avoiding predator attacks. Turtles, in addition, may perform these mid-water dives (type 1 and 2) in order to avoid unstable conditions at the sea surface, e.g. pitching and rolling due to wave action (Minamikawa *et al.* 1997, 2000). Sea snakes have indeed been shown to perform more of such mid-water dives when surface water was turbulent (Rubinoff *et al.* 1986).

Because of their nocturnal prevalence and their similarities in shape with U-shaped resting dives, it is tempting to think that type 1 dives could be mid-water resting dives. Indeed, inter-nesting Green turtles from Ascension Island and Cyprus preferentially rest during night-time (Hochscheid *et al.* 1999, Hays *et al.* 2000a), and also, the present study showed that the speed of travel declines when the proportion of time spent mid-water diving increases. Minamikawa *et al.* (1997, 2000) hypothesised that type 1 dives performed by Loggerhead sea turtles were resting dives, since there was a positive relationship between dive depth and duration, and since the speed during the gradual ascent was zero in 50% of these dives. However, the stall speed of the sensor used in that study was of 0.3 m s^{-1} (= 1.08 km/h). Such a high threshold is likely to fail detecting forward movement (i.e. speed) during the gradual ascent, whilst in reality the turtle could be swimming at a speed somewhat slower than the threshold. In contrast, Hochscheid *et al.* (1999) used activity sensors to reveal that Green turtles from Cyprus remain active throughout the different phases of these mid-water dives.

If type 1 dives are not resting dives *per se*, then their overall metabolic rate should be greater than in resting dives. Hays *et al.* (2000a) reported the mean depths and durations of U-shaped resting dives to the seabed performed by two inter-nesting Green turtles at Ascension Island (the data was obtained using TDRs). In chapter 3 (pp. 92-129, data was obtained using SL-TDRs), the mean depths and durations of U-shaped dives were calculated for four inter-nesting turtles at Ascension Island in 2001. If the data from these two studies is pooled, the mean resting depths of Green turtles at Ascension (mean = 15.1 m, SD = 1.9 m, $N = 6$ turtles) is not significantly different (unpaired t-tests, $p > 0.05$) from the mean depths of type 1 dives for the present study (mean = 15.2 m, SD = 3.0 m; $N = 5$ turtles). In contrast, the mean durations of type 1 dives (mean = 28.5 min., SD = 1.6 min., $N = 5$ turtles) are significantly shorter (unpaired t-tests, $p < 0.05$) than the mean durations of U-shaped resting dives (mean = 36.4 min., SD = 7.5 min., $N = 6$ turtles). Similar mean dive depths indicate that lung volumes upon leaving the surface (volume of air required to achieve neutral buoyancy at depth) and the associated oxygen stores are similarly sized, both for type 1 dives and U-shaped resting dives. Differences in mean durations, however, suggest that oxygen stores become depleted faster during type 1 dives than during U-shaped resting dives, most probably as a result of differences in overall activity levels. This indicates that the metabolic rate during type 1 dives is probably greater than the metabolic rate during a resting dive.

There are a very limited range of speeds of movement, for a migrant travelling a given horizontal distance, that will result in an optimal energy expenditure (Schmidt-Nielsen 1998). Swim faster or slower than such a ‘speed of minimum cost of transport’, and the energetic cost of covering a given horizontal distance increases disproportionately. From this point of view, resting at depth during long-distance travel appears an inadequate strategy when dealing with limited energy reserves. Indeed, such a resting behaviour would be accompanied by a sharp decrease in the overall speed of travel, which would then increase travel time and increase the energy allocated to fuel basal metabolic functions, hence another reason pointing towards type 1 dives not being resting dives.

In spite of being mid-water resting dives, type 1 dives may be some sort of mid-water travelling dives, during which relatively slow-speed movements (potentially undetected by speed sensors) would take place during the gradual ascent phase. During these dives, turtles could still rest to an extent (in agreement with their tendency to rest nocturnally, similarly to when they perform U-shaped resting dives at Ascension Island). Above all, this would explain the decrease in speed of travel that coincides with greater time spent performing type 1 dives. As previously suggested (Graham *et al.* 1987 for Sea snakes and Hochscheid *et al.* 1999 for Green turtles), it is possible that turtles make use of the positive buoyancy of their expanding lungs, in order to passively fuel forward movement. These authors add that a horizontal flipper beat would result in an even greater forward movement. Indeed, some animals (such as negatively buoyant fish), are thought to use their negative buoyancy to passively drift downwards, whilst subsequently actively swimming back up, because swimming the same horizontal distance directly is more energetically costly (Weihs 1973).

As well as minimising time at the surface (predator- and turbulence-avoidance), type 1 dives probably reflect an energy-saving swimming behaviour. Also, there may be a variety of metabolic rates for type 1 dives, which will depend on the relative proportions of resting versus slow-speed swimming they perform during any one type 1 dive. Finally, Green turtles have recently been shown to consume scyphozoans (Heithaus *et al.* 2002), suggesting that type 1 dives (and this can be extended to type 2 dives) may reflect turtles foraging on such prey. There is, however, a crucial lack of information on the presence and vertical distribution of scyphozoans in the waters around Ascension Island, and this possible foraging function of type 1 and 2 dives needs further investigation.

Role of type 2 dives

Hays *et al.* (2001a) reported that type 2 dives had significantly deeper maximum depths than type 1 dives, but that the mean depths of the two types of dives were fairly comparable. This was simply because the effect of the deeper excursion during type 2 dives (before the gradual ascent) was attenuated when looking at the mean values. In contrast, for all but one individual (turtle C), type 1 dives lasted significantly longer than type 2 dives. As discussed above, comparable mean depths, but differences in mean duration, suggest that for similarly-sized lung volumes (and oxygen stores) upon leaving the surface, oxygen stores may become depleted faster during type 2 dives than during type 1 dives. This is consistent with the fact that type 2 dives have greater mean rates of vertical movement during the gradual ascents, than type 1 dives, suggesting that oxygen tends to become depleted faster during type 2 dives, most probably as a result of greater overall activity levels. The presence of the deeper excursion during type 2 dives, and its associated energetic cost, may also partly explain this discrepancy in duration, and hence in metabolic rate, between type 1 and 2 dives.

Type 2 dives are likely to reflect a complex combination of surface avoidance (predator and turbulence), possible foraging on scyphozoans, with some energy-saving swimming during the gradual ascent (Hochscheid *et al.* 1999). Moreover, there is now compelling evidence pointing towards type 2 dives also being part of an active searching behaviour. Firstly, unlike type 1 dives that are mainly nocturnal, type 2 dives occur at any time of the day, although it is true that the fastest mean ascent rates were for day-time dives. Secondly, the deeper excursions of type 2 dives show extremely variable lengths (differences between mean and maximum depths reached up to 44 m) as if the turtles increased the vertical distance scanned during the deeper excursions. This has also been suggested for Sea snakes, where deeper excursions were thought to be an exploration of the water column (Graham *et al.* 1975, 1987). Finally, type 2 dives tend to be more frequent during critical moments of the homing journeys, i.e. just after release in the ocean and during the final, island-directed legs of the homing journeys (and the middle, island-directed leg of turtle B).

It is striking that four out of the five individuals performed their deepest type 2 dives (sometimes deeper than 60 m) during the final, island-directed legs of their homing journeys (turtle B also performed relatively deeper type 2 dives during the middle island-directed leg of its journey). The latter is also shown by the ‘other’ mid-water dives (i.e. dives which are not type 1 or 2 dives), which could be deeper than 70 m during the final, island-directed legs of the journeys. The fact that the deep type 2 dives (and ‘other’ dives) at the very end of the homing trips were followed, towards reaching the island, by comparatively deep flat-bottomed dives strongly indicates that type 2 dives had function in searching the water column, which resulted in them detecting the seabed upon arrival in Ascension Island. Then, performing deep flat-bottomed resting dives upon arrival in the vicinity of the island reflects an affinity for the sea floor. Such behaviour is likely to provide additional camouflage in the predator-rich waters around the island, until more ‘ordinary’ resting depth (15-20 m) are reached and a more ‘normal’ resting behaviour can resume.

Further aspects of the diving behaviour

During bouts of type 1 or 2 dives, the lengths of dive intervals were unrelated to the preceding or following dive durations. Turtles did spend very variable proportions of the pre- and post- dive intervals at or close to the surface (on average, between 34% and 46% of the dive interval), and that dives lasted longer when these proportions increased (except one turtle). The post-dive interval is considered to be the time necessary to physiologically recover from a dive and to prepare for a next one (Chappel *et al.* 1993). Turtles spent time at, or close to, the surface at the start of the dive interval, or at its end, or at both times. This makes it difficult to attribute this surface time to the influence of either the previous (as a recovery) or following (in preparation of) dive of the bout (not to mention more indirect and complex interactions with other dives of the bout).

All five individuals could spend up to 100% of their dive intervals at or close to the surface, but the associated lengths of time were in reality quite short (i.e. less than 4 minutes on average), and comparable to the post-dive intervals of Green turtles performing resting dives at Ascension Island (Hays *et al.* 2000a). The results suggest that, although type 1 and 2 dives and the associated pre- and post- dive intervals are inter-related, turtles will not exceed their aerobic dive limits during these dives, hence avoiding long surface-recovery times.

Conclusions

A clear dichotomy is apparent in the diving of this long-distance migrant: (1) short and shallow travelling dives (mostly during day-time) are most probably used to maximise horizontal movement, whilst (2) mid-water diving (type 1 & 2 dives) would serve several functions. They would involve some resting as well as some horizontal movement (though at slower speed, but presumably enough to avoid a significant rise of cost of transport), as well as allowing to minimise time at the surface (hence avoiding predators and turbulence), and possibly foraging on scyphozoans. Type 2 dives may also allow scanning the water column, as part of a searching behaviour.

Because short and shallow travelling dives may incur a relatively high energetic cost, there may exist a physiological reason preventing turtles to maintain a relatively fast speed of travel throughout long-distance travel. Bouts of mid-water diving may offer an alternative to stopping horizontal movement altogether: hence slow-speed swimming would permit to keep the overall basal metabolic costs down, as well as providing a certain amount of rest, preferentially at night (because of the intrinsic diurnal activity cycle in this species).

It may be argued that diving was affected by experimental displacement. However, the diving that has been recorded in the present study is very consistent with submergence and depth information collected *via* satellite telemetry, during the post-nesting migration of Ascension Island Green turtles, back to Brazil (Hays *et al.* 2001a, Hays *et al.* 1999). Moreover, the results of the present study are likely to shed more light on previous and future studies that have or will investigate diving behaviour of shallow diving sea turtles using satellite telemetry, since summarised information will be better understood and interpreted.

CHAPTER 2

Descent and ascent tactics of the Green turtle during mid-water diving

INTRODUCTION

Air breathing aquatic and semi-aquatic animals can dive with remarkable ability (e.g. Sea snake, *Pelamis platutus*: Rubinoff *et al.* 1986; Sea otter, *Enhydra lutris*: Williams 1989; Elephant seal, *Mirounga sp.*: Campagna *et al.* 1995, Davis *et al.* 2001; Northern Rockhopper penguin, *Eudyptes chrysocome moseleyi*: Cherel *et al.* 1999), and different dive profiles have been associated with fundamental activities such as resting, feeding, hunting, exploration, travel or transit (see for example Chappel *et al.* 1993, Le Bœuf *et al.* 1993, Schreer *et al.* 2001). As air-breathing animals, when diving, rely on limited oxygen reserves, stored in their lungs, blood and tissues (Williams *et al.* 1999), it might be expected that divers would evolve behavioural strategies so as to optimise oxygen utilisation during submergence. The optimisation of swimming and diving with regards to limited oxygen reserves has attracted a keen interest over the past years. For instance, many marine animals have been shown to migrate and/or perform their daily movements (between different areas or food patches) by swimming at the speed that minimises their cost of transport (e.g. North American mink, *Mustela vison*: Williams 1983; Thompson *et al.* 1993; Bottlenose dolphin, *Tursiops truncatus*: Williams *et al.* 1993). Also, many studies have looked at swimming tactics that promote energy savings, such as porpoising and wave-riding (Au & Weihs 1980, Blake 1983, Williams *et al.* 1992), or such as the use of interrupted patterns of swimming instead of constant propulsion (e.g. burst and glide swimming, gliding using buoyant forces) (Skrovan *et al.* 1999, Williams *et al.* 1999, Williams *et al.* 2000).

During the course of a dive, the descent and ascent phases may be part of a specific activity, for example when they form part of a V-shaped travelling dive (e.g. Grey seal, *Halichoerus grypus*: Thompson *et al.* 1991), or when exploring the water column for potential prey (e.g. Gentoo penguin, *Pygoscelis papua*: Wilson *et al.* 1996). However, descent and ascent phases can also primarily represent a transit movement between the location of the oxygen supply (the surface) and the location of the activity, for example benthic foraging (e.g. Emperor penguin, *Aptenodytes forsteri*: Rodary *et al.* 2000), resting on the sea bed (e.g. Green turtle: Hochscheid *et al.* 1999), or foraging on a prey patch (e.g. Thompson & Fedak 2001). Because descent and ascent segments of dives are intrinsic components of the underwater activity of diving animals, and because oxygen stores are limited during diving, evolution would be expected to select for energetically efficient diving tactics optimising performance during these two phases. If the energetic cost of commuting is minimised, then the proportion of time that may be spent at the location of the activity (e.g. benthic foraging) will be maximised, *via* prolonging aerobic metabolic support during submergence.

Aquatic animals may be influenced by buoyancy, whose intensity and orientation are directly dictated by the density of the animal compared to that of the water (Alexander 1990). The influence of changes in body buoyancy (these changes may be caused by seasonal changes in body composition) on diving has recently generated much interest (e.g. Northern Elephant seal: Crocker *et al.* 1997; Grey seal: Beck *et al.* 2000). In the case of relatively deep divers, such as some phocid seals, the body buoyancy is principally determined by body mass and the ratio of adipose tissue to lean body tissue (Webb *et al.* 1998, Beck *et al.* 2000). Fat and other body tissues are essentially incompressible compared to air (Wilson *et al.* 1992, Fish 2000). In contrast, the reduction of gas-filled cavities (i.e. lungs, pelage, plumage) with hydrostatic pressure, reduces up-thrust and creates a more dynamic component of buoyancy, that varies with depth (Nowacek *et al.* 2001). Relatively ‘shallow’ divers such as the Sea snake (Graham *et al.* 1987), Sea otter and Muskrat (Fish 2000), or most species of hard-shell sea turtles (Milsom 1975, van Dam & Diez 1996, Lutcavage & Lutz 1997), inhale before submerging (Kooyman & Ponganis 1998). Consequently, lung volume will be a major factor altering their buoyancy underwater (Jackson 1969, Skrovan *et al.* 1999). For these animals, the energetic implications of dynamic changes in buoyancy with depth are of particular importance since metabolic rate will be greatly influenced by the effort required, for example, to reach and maintain depth (Lovvorn & Jones 1991b, Lovvorn *et al.* 1991). For instance, Lesser scaups (*Aythyta affinis*) can allocate up to 95% of the total mechanical energy expended during a dive to work against their positive buoyancy (Stephenson *et al.* 1989).

For relatively shallow divers that inhale before submerging and that usually dive no deeper than their depth of neutral buoyancy, the energetic cost of overcoming up-thrust will be more marked during descent than ascent (Stephenson *et al.* 1989, Lovvorn & Jones 1991a, 1991b, Lovvorn *et al.* 1991). Furthermore, the effort required to overcome buoyancy resistance will be greatest upon leaving the surface, before hydrostatic pressure (which increases with depth) has compressed the lungs (Wilson *et* *al.* 1992). Conversely, up-thrust may facilitate ascending movement: some water birds are even capable of rising passively to the surface using their positive buoyancy (Wilson *et al.* 1992). Because the up-thrust caused by the presence of air in the lungs will vary with depth, it is predicted that shallow divers will have evolved depth-sensitive descent and ascent tactics for cost efficient vertical movement.

The energy expended in overcoming up-thrust at the start of a dive could be reduced if the proportion of time spent at locations in the water column where up-thrust is greatest, is reduced. This may be achieved by using relatively steep descent angles at the start of dives (as Green turtles are known to use, Glen *et al.* 2001), and such steep descent angles will probably be associated with relatively faster rates of vertical movement (i.e. descent rates, not the actual swim speed, the latter being a combination of vertical and horizontal components). As the descending movement progresses and up-thrust declines (*via* lung compression with depth), the need for minimising the proportion of time spent fighting up-thrust is expected to become less and less critical and therefore, the descent rates may decelerate (only rates of vertical movement are considered, without any assumption made about the actual swim speed). Alternatively, shallow divers may have difficulties in overcoming the high buoyancy resistance upon leaving the surface, resulting in rather slow initial descent rates. Meanwhile, as up-thrust subsequently declines, descending movement could then be facilitated, potentially resulting in accelerating descent rates. In contrast, if vertical movement is facilitated by up-thrust, one might expect an acceleration of the ascending movement (i.e. accelerating ascent rates, still no assumption is made about the actual swimming speed), in line with lung expansion.

Although studies on diving animals generally mention descent and ascent rates of vertical movement (e.g. Loggerhead turtle: Sakamoto *et al.* 1990; Gentoo penguin: Wilson *et al.* 1996; Northern Elephant seal: Webb *et al.* 1998; Southern Rockhopper penguin, *Eudyptes chrysocome filholi*: Tremblay *et al.* 2000), short-term variations of these rates are rarely investigated in detail (but see van Dam & Diez 1997 for the Hawksbill turtle, *Eretmochelys imbricata*). Moreover, very few studies have investigated the short-term variations in the rates of vertical movement with dynamic changes in buoyancy with depth (e.g. Northern Bottlenose whale, *Hyperoodon ampullatus*: Hooker & Baird 1999; Brunnich's guillemot, *Uria spp.*: Lovvorn *et al.*

1999; Right whale, *Eubalaena glacialis*: Nowacek *et al.* 2001). Three reasons can explain this knowledge gap. Firstly, some divers actually descend or ascend at fairly constant vertical rates, in which case, concentrating on mean rates is adequate and sufficient. Secondly, when depth loggers are programmed to sample depth at relatively long time intervals (i.e. every minute or so), mean rates are more reliable dive parameters to concentrate on, since short-term variations of descent and ascent rates may not be detectable. Finally, if neutral buoyancy is reached early in the descent, the energetic cost of overcoming up-thrust at the start of the descent may actually be negligible, when compared with the overall energetic cost of descent (and conversely for ascent). This may explain why for relatively deep divers such as Elephant seals, most penguins and whales, or even the Leatherback sea turtles (*Dermochelys coriacea*) (Eckert *et al.* 1986, Boyd 1993, Kooyman & Ponganis 1998), rates of vertical movement are usually averaged over the entire descent or ascent phases of dives. Moreover, some divers, such as phocid seals (Webb *et al.* 1998) and Humboldt penguins (*Spheniscus humboldti*, Butler & Woakes 1984), are known to exhale at the start of deep dives, an activity that minimises the effect of up-thrust near the surface, as well as preventing nitrogen narcosis and the associated risks of decompression sickness (Kooyman & Ponganis 1998).

There have been relatively few comprehensive studies investigating which descent and ascent tactics would minimise transit costs when up-thrust changes with depth. The Green turtle is a relatively tractable group for testing predictions on the optimisation of descent and ascent tactics during shallow diving. Indeed, this turtle is thought to adjust its lung volume before submerging, so as to become neutrally buoyant at depth (Hays *et al.* 2000a, 2001a). During these dives, the Green turtle would be expected to optimise its activity during transit through the zone of positive buoyancy. Indeed, this would minimise the energetic cost of transit and, in turn, permit longer time at depth. Whilst short duration dives permit great flexibility in activity (as the impact on oxygen stores is relatively low), dives of relatively longer duration are more likely to involve energy conserving tactics since oxygen balance is more of a limiting factor (Skrovan *et al.* 1999, Williams *et al.* 1999). High-resolution pressure sensors were used to see whether descent and ascent rates vary with depth, during transit between the surface and the depth of neutral buoyancy. The energetic implications for descent and ascent tactics of modelled changes in lung volume with depth were discussed.

MATERIALS & METHODS

‘*Fieldwork & Diving information*’, given in chapter 1.

Rates of vertical movement

Both type 1 and 2 dives (these dives have been described in chapter 1, pp. 33-68, and in Hays *et al.* 2001a) comprise a fast descent to a ‘maximum depth’ (points A in figure 2-1 A, p. 75), then a gradual ascent (during which turtles are thought to be neutrally buoyant), before a final, more rapid ascent to the surface. Type 2 dives differ slightly from type 1 dives, because the gradual ascent phase is preceded by the turtle descending deeper and then ascending rapidly to a depth similar to the start of the gradual ascent of type 1 dives. Because of this difference between type 1 and type 2 dives, their descent phases were investigated separately. ‘Minimum bottom depth’ (points B in figure 2-1 A, p. 75) marks the end of the gradual ascent (before the start of the rapid ascent phase). Only the vertical rates of movement during the phases of these dives when turtles are positively buoyant, i.e. during the descent and rapid ascent phases, were investigated (the vertical rates of movement during the gradual ascent phase have been investigated in chapter 1, pp. 33-68). These vertical rates of movement were derived from the pressure readings made by the TDRs during these phases of the dives. The descent phase of a type 1 or 2 dive included the depth readings that were made during the time between the surface and point A of the dive, whilst the ascent phase included the depth readings that were made during the time between point B of the dive and the surface.

The relative position of a turtle during a descent phase was described by the ‘percentage of maximum depth’, which was the depth of the turtle at the time divided by the value of the maximum depth of that dive (points A in figure 2-1 A, p. 75). Similarly, the relative position of a turtle during an ascent phase was described by the ‘percentage of minimum bottom depth’, which was the depth of the turtle divided by the value of the minimum bottom depth of that dive (points B).

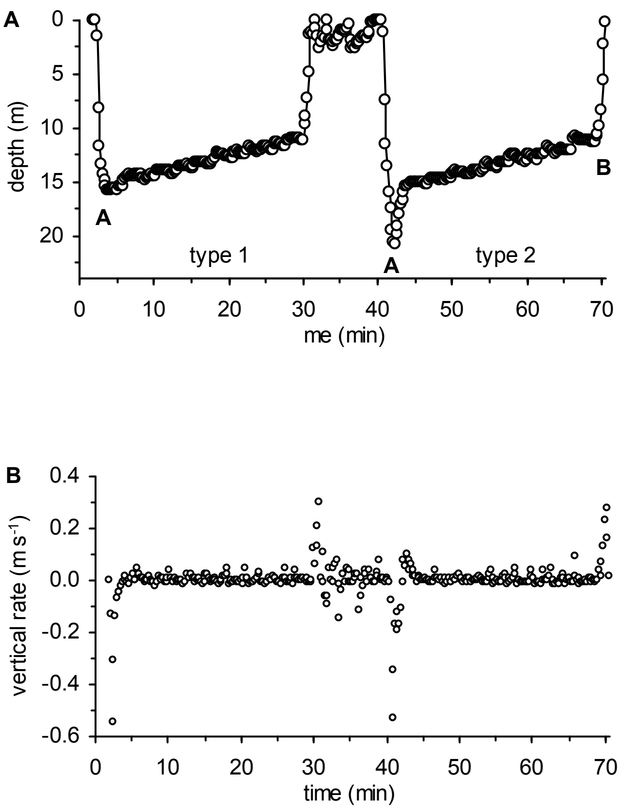


Figure 2-1. (A) Typical examples of type 1 and type 2 dives. Point A is the end point of descent (maximum depth) and point B is the end point of the gradual ascent (minimum bottom depth). (B) The rates of vertical movement during the course of the two dives shown in (A). Positive values of the rates of vertical movement in figure 2-1 B are ascent rates, whilst negative values are descent rates.

The vertical rate of movement (V, in m s^{-1}) during one sampling interval was defined as the ratio of the vertical distance between two successive pressure readings to the length of the sampling interval (i.e. 12 seconds):

$$V = (\text{depth }[n+1] - \text{depth }[n]) / 12$$

For each sampling interval, the rates of vertical movement for the descent phases (Vd) and ascent phases (Va) of type 1 and type 2 dives (figure 2-1 A, p. 75) were calculated. Figure 2-1 B (p. 75) shows the rates of vertical movement that were derived from the type 1 and type 2 dives shown in figure 2-1 A. As turtles may have left the surface at any time during the 12 seconds separating the first two pressure readings of a descent phase, or may have reached the surface at any time during the 12 seconds separating the last two pressure readings of an ascent phase, the resulting descent or ascent rates were likely to be underestimated, and thus were discarded.

RESULTS

The body masses of the five displaced turtles ranged from 145.5 kg to 189 kg (mean = 158.5 kg) and a total of 350 dives were analysed (table 2-1, p. 77). A random selection of the type 1 and 2 dives analysed in chapter 1 were selected for analysis (this was to avoid cluttered graphs). For each turtle, the selection of dives was based on a computer-generated list of random numbers.

Rates of vertical movement during type 1 & 2 dives

During the descent phases of type 1 dives, fast descent rates of vertical movement were recorded upon leaving the surface (at 0 – 40% of maximum depth). Descending movement progressively decelerated with greater depths (40 – 100% of maximum depth) until maximum depth was reached (figure 2-2 A-E, p. 78). Descent rates significantly declined as turtles were relatively deeper in the descent phases of type 1 dives.

The descent behaviour during the descent phases of type 2 dives presented a pattern similar to the one of type 1 dives, with fast descent rates occurring at the start of the descent phases, and progressively slower descent rates with greater depths (figure 2-3 A-E, p. 79). However, around the depth of 19-20 m, there was a change in the descent

Turtle	Type 1	Type 2	Body mass (kg)
A	80	8	152.0
B	50	32	154.0
C	63	9	189.0
D	19	17	152.0
E	34	38	145.5

Table 2-1. Type 1 and 2 dives analysed in this chapter, and body masses (kg) of the five Green turtles.

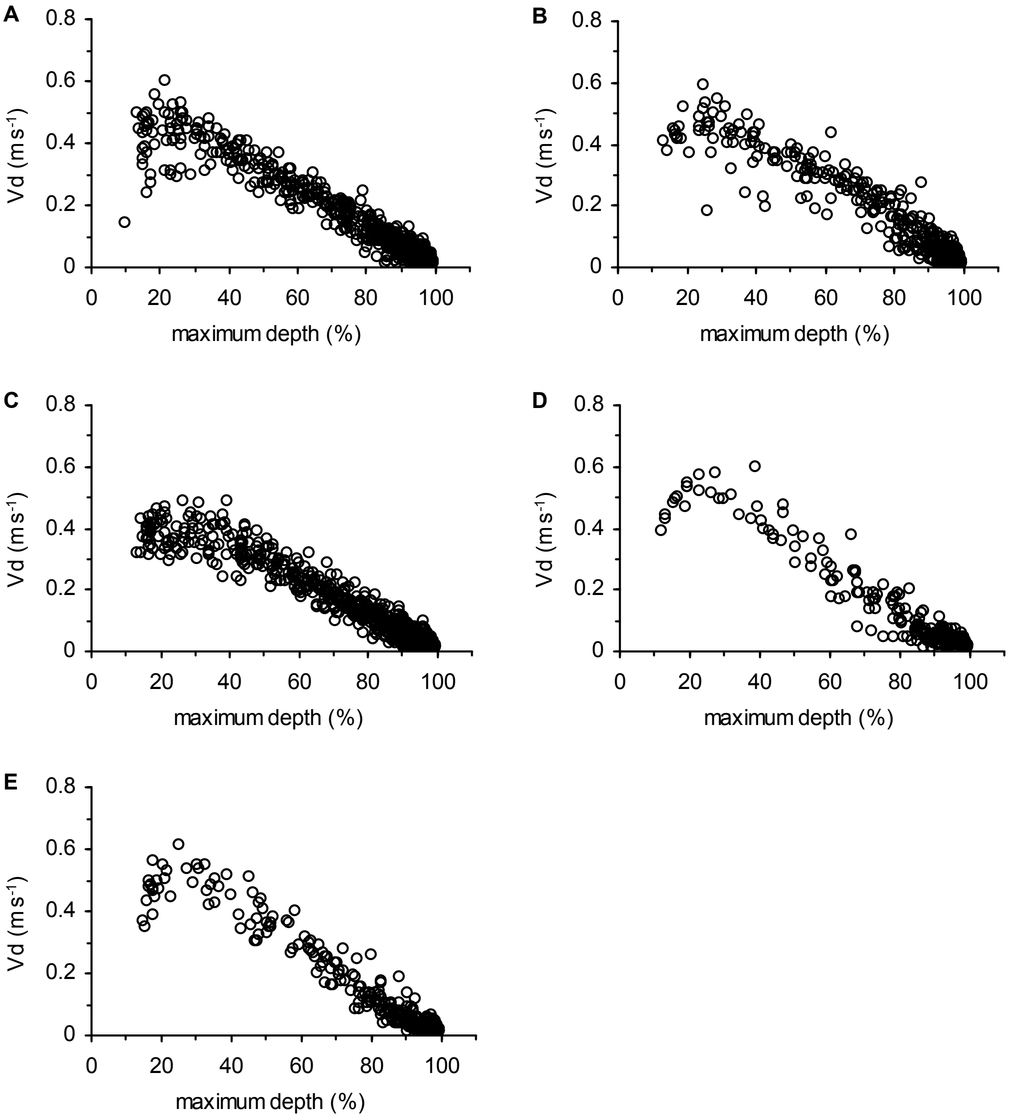


Figure 2-2. During type 1 dives, the relationship between descent rates and the relative position during descent (percentage of maximum depth; 0% is at the surface). A, B, C, D & E are for turtles A to E, respectively. Regression analyses: turtle A: $F_{0.05,\ 1,\ 724} = 8446.0$, $r^2 = 0.92$, $p < 0.0001$; turtle B: $F_{0.05,\ 1,\ 371} = 3036.3$, $r^2 = 0.89$, $p < 0.0001$; turtle C: $F_{0.05,\ 1,\ 801} = 10535.0$, $r^2 = 0.92$, $p < 0.0001$; turtle D: $F_{0.05,\ 1,\ 213} = 1751.4$, $r^2 = 0.89$, $p < 0.0001$; turtle E: $F_{0.05,\ 1,\ 284} = 3637.6$, $r^2 = 0.92$, $p < 0.0001$.

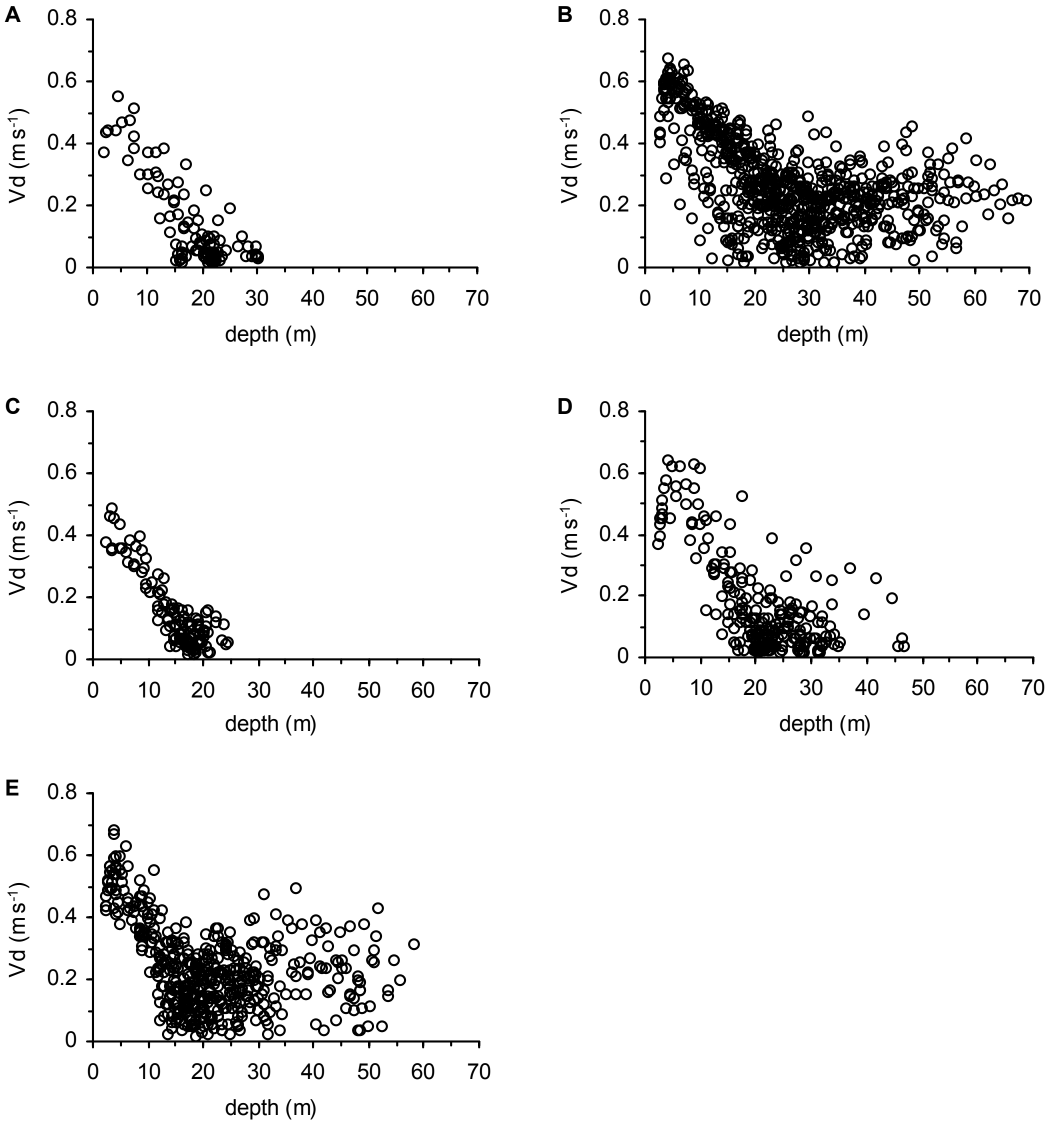


Figure 2-3. During type 2 dives, the relationship between descent rates and the depth during descent. A, B, C, D & E are for turtles A to E, respectively.

pattern for all five turtles, with the descent rates seemingly becoming independent from depth. This change was particularly clear for turtles B & E (figure 2-3 B & E, p. 79).

During the ascent phases of type 1 and 2 dives, relatively slow ascent rates were recorded upon leaving the depth of neutral buoyancy (at 80 – 100% of minimum bottom depth), whilst ascending movement progressively accelerated with decreasing depths, until the surface was reached (figure 2-4 A-E, p. 81). Ascent rates were found to accelerate significantly as depths were shallower.

Overall, short-term variations in the rates of vertical movement (descent and ascent) when the turtles were thought to be positively buoyant (i.e. at depths shallower than about 19-20 m) were similar in pattern to the changes in hydrostatic pressure and possibly lung volume with depth. Potential relationships between changes in lung volumes with depth and short-term variations in the rates of vertical movement were investigated through the modelling of lung volumes during diving.

Modelling of lung volumes during type 1 & 2 dives

In order to estimate lung volumes during the descent and ascent phases of type 1 and 2 dives, a model described in Hays *et al.* (2000a) was adapted. This previous model attempted to estimate lung volumes (upon leaving the surface) for turtles achieving neutral buoyancy at various depths of the sea bed. Turtles were assumed not to exhale air during mid-water dives (van Dam & Diez 1997, Hays *et al.* 2000a), and 'LungVol' (in litre) was defined as the lung volume during one sampling interval. Assuming that the compression of air in the respiratory system was unopposed by structural resistance of the body wall (Lovvorn & Jones 1991a), lung volume varied (in accordance with Boyle's Law) with the surrounding hydrostatic pressure (Berkson 1967). The main assumption of the model was that adult Green turtles from Ascension Island achieved neutral buoyancy at 19 m if they inhaled fully upon leaving the surface (Hays *et al.* 2000a), and that the lung capacity (in litre, l) of Green turtles was 9.4% of the turtle's body mass in kilograms (Berkson 1966). The reasons behind the '19 m hypothesis', which are clarified in the Discussion, are mainly behavioural, and not based on considerations of static lift versus body mass.

The hydrostatic pressure (Press [n], expressed in atmosphere absolute, ata) at depth [n] is, by definition:

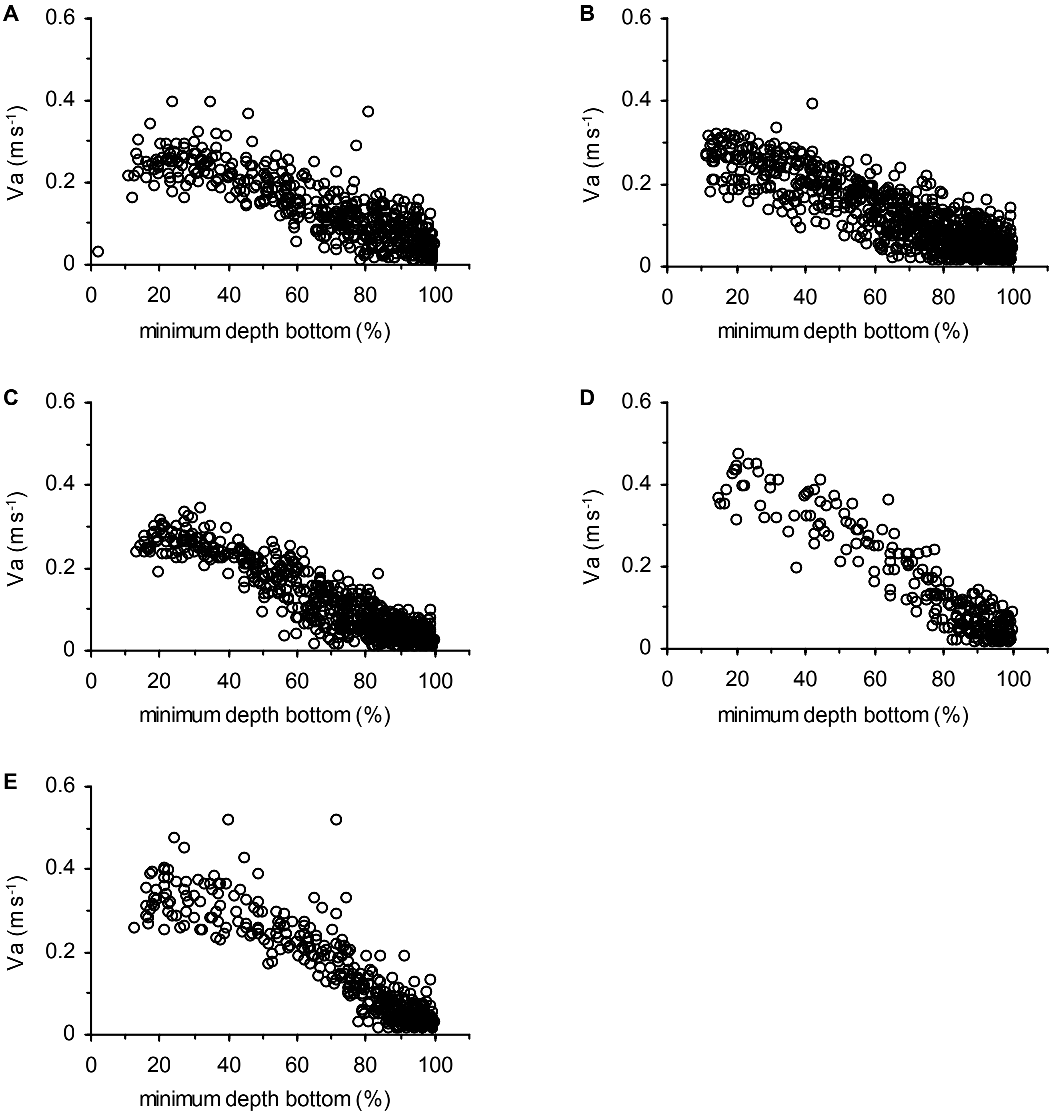


Figure 2-4. During type 1 and 2 dives, the relationship between ascent rates and the relative position during ascent (percentage of minimum depth bottom, 0% is at the surface). A, B, C, D & E are for turtles A to E, respectively. Regression analyses: turtle A: $F_{0.05,\,1,\,490} = 1057.3$, $r^2 = 0.68$, $p < 0.0001$; turtle B: $F_{0.05,\,1,\,917} = 2749.2$, $r^2 = 0.75$, $p < 0.0001$; turtle C: $F_{1\text{-}771} = 4313.1$, $r^2 = 0.84$, $p < 0.0001$; turtle D: $F_{0.05,\,1,\,238} = 1647.7$, $r^2 = 0.87$, $p < 0.0001$; turtle E: $F_{0.05,\,1,\,429} = 1857.4$, $r^2 = 0.81$, $p < 0.0001$.

$$\text{Press [n]} = 1 + \text{Absolute Depth [n]} / 10$$

and the lung volume (LungVol [n]) at that depth is:

$$\text{LungVol [n]} = (\text{LungVol [surface]} \times \text{Press [surface]}) / \text{Press [n]}$$

where LungVol [surface] is the lung volume upon submerging and Press [surface] is the atmospheric pressure at the water surface (Press [surface] = 1 ata; Milsom 1975).

For example, a 150 kg turtle has a lung capacity of 150 x 0.094 = 14.1 litres of air, and becomes neutrally buoyant at 19 m if it left the surface with 14.1 l of air in its lungs. Therefore, the lung volume at 19 m (LungVol [19 m]) is:

$$\text{LungVol [19 m]} = \text{Lung Capacity} \times \text{Press [surface]}) / \text{Press [19 m]}$$

$$= 14.1 \times 1 / 2.9 = 4.8 \text{ l of air}$$

According to the model, this turtle attains neutral buoyancy at depth, if its lungs are compressed down 4.8 l of air, which can be achieved at 19 m if the turtle left the surface with fully inflated lungs, or shallower than 19 m if it left the surface with less than 14.1 l of air in its lungs. Hence, the depth of neutral buoyancy is closely associated with the lung volume upon leaving the surface (Minamikawa *et al.* 1997, 2000).

During the gradual ascent of type 1 and 2 dives, Green turtles are thought to be neutrally buoyant, and they gradually ascend in the water column in order to compensate for the buoyancy loss resulting from oxygen being taken from the lungs, without a replacement by carbon dioxide (Hays *et al.* 2001a). From the start until the end of the gradual ascent, the lung volume is hence kept constant. For the example given above, it would be equal to 4.8 l of air. Some type 1 and 2 dives had a gradual ascent starting deeper than 19 m, but such dives were relatively rare. For each type 1 or 2 dive, by using the start and end points of the gradual ascent phase, it was possible to estimate the lung volumes corresponding to the depth of each sampling interval during the descent and ascent phases of the dive. Finally, mass-specific lung volume (i.e. LungVol / mass, in l kg^{-1}) were used as an indicator of the buoyancy state of a turtle.

The five turtles appeared to have behaved in very similar ways during the descent phases of their type 1 dives (figure 2-5 A, p. 83, combines the data from the five turtles). There was a clear deceleration with decreasing mass-specific lung volumes during type 1 mid-water dives. In other words, increased positive buoyancies near the surface were associated with faster rates of descent. In this way, turtles appeared to have minimised the proportion of time spent in the water column where they were the most

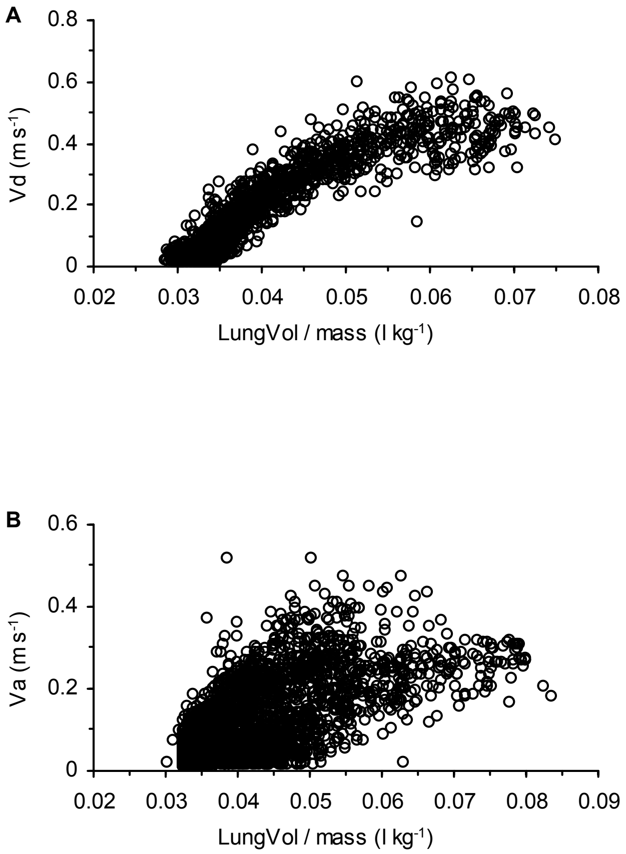


Figure 2-5. The relationships (A) between descent rates and mass-specific lung volumes during type 1 dives, and (B) between ascent rates and mass-specific lung volumes during type 1 and 2 dives (*N* = 5 turtles for both figures).

positively buoyant. They achieved this by descending relatively quickly when near the surface, but slowing when positive buoyancy decreased due to lung compression. Although less clear, the ascending movement during type 1 and type 2 dives accelerated with increasing mass-specific lung volumes, i.e. with increasing levels of up-thrust due to lung expansion (figure 2-5 B, p. 83, combines the data from the five turtles). For both descent and ascent phases, changes in lung volume appeared closely linked to short-term changes in the rates of vertical movement.

This simple modelling of lung volumes was based on the assumption that turtles become neutrally buoyant at 19 m if they left the surface with fully inflated lungs. The consequences of varying this ‘maximum’ depth of neutral buoyancy could be tested, to check whether the relationships between mass-specific lung volumes and the rates of vertical movement would change. The same calculations described above were run, for each turtle separately, for substantially different maximum depths of neutral buoyancy (10 m, 19 m and 30 m). The results of such a sensitivity analysis are shown for turtle A in figure 2-6 (p. 85). Although there seems to be more scatter in the relationship when the maximum depth of neutral buoyancy was shallow (here 10 m), the general shape of the relationship was not altered significantly as a result of substantial changes in the maximum depth of neutral buoyancy (from 10 to 30 m). In all three cases, descending remained fast when up-thrust was great (i.e. near the surface), whilst descending decelerated with decreasing levels of up-thrust (as lungs became compressed). Similar results were obtained for the relationships between ascent rates and mass-specific lung volumes when the depth of neutral buoyancy was altered in such ways.

DISCUSSION

The maximum depth of neutral buoyancy

Ascension Island Green turtles are thought to be capable of passive resting on the sea bed. To do so, they are thought to adjust their lung volume upon leaving the surface in order to achieve neutral buoyancy when reaching the sea bed (in practice, they would be slightly negatively buoyant; Hays *et al.* 2000a). By being neutrally buoyant when on the sea bed, turtles do not need to expend any locomotor energy to maintain depth. Besides, since the depth of neutral buoyancy will be determined by the

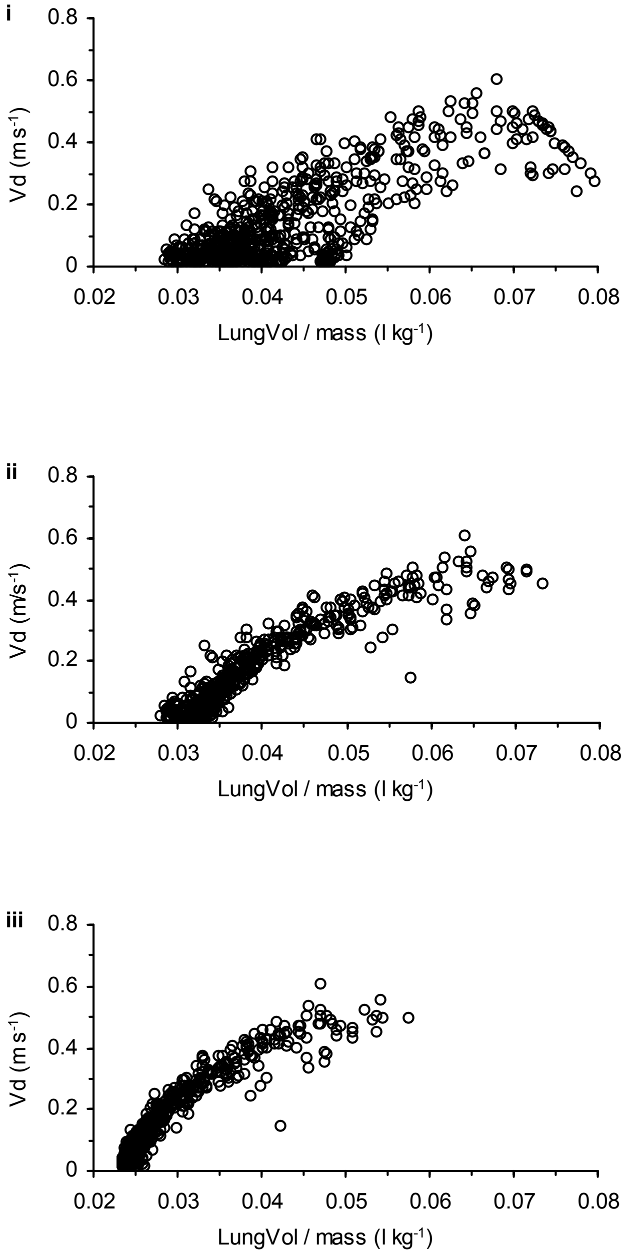


Figure 2-6. The relationship between descent rates and the mass-specific lung volume during descent. Sensitivity analysis (turtle A, see text for details) if the depth of neutral buoyancy when leaving the surface with fully inflated lungs is (i) 10 m, (ii) 19 m or (iii) 30 m.

lung volume prior to the dive, the lung capacity will eventually limit the depth range at which neutral buoyancy can be achieved (Minamikawa *et al.* 1997, 2000). Hence, the deepest resting depths should correspond to the maximum depth at which turtles can attain neutral buoyancy. Resting dives to the sea bed being rarely deeper than 19 m at Ascension Island (N = 6 Green turtles), Hays *et al.* (2000a) hypothesised that neutral buoyancy is achieved at the critical depth of 19 m if the turtle has left the surface with fully inflated lungs.

During the gradual ascent of type 1 and 2 dives, turtles are also thought to be neutrally buoyant (Hays *et al.* 2001a). Since the gradual ascents of type 1 and 2 dives were rarely deeper than 19 m (see chapter 1 and Hays *et al.* 2001a), this represents additional behavioural information pointing towards 19 m being the maximum depth at which Green turtles can attain neutral buoyancy. According to this, when turtles are deeper than the start point of the gradual ascent (as it occurs during the deeper excursion of type 2 dives), they are negatively buoyant, whilst they are neutrally or positively buoyant at any depth shallower than this point (upper part of the descent phase, and rapid ascent phase).

During the descent phases of type 1 dives, and when shallower than about 19 m during the descent phases of type 2 dives, the current study has found that the descent rates were depth-dependent, and most probably highly dependent on the level of positive buoyancy. In contrast, during the descent phases of type 2 dives when deeper than about 19 m (this corresponds to the deeper excursion during these dives), a similar relationship between descent behaviour and depth was not found. This discrepancy in descent behaviour between type 1 and 2 dives provides additional support for the depth of 19 m being the maximum depth at which Green turtles of Ascension can attain neutral buoyancy. At depths shallower than around 19 m, turtles are more or less positively buoyant and adapt their descent rates to deal with changes of buoyancy. At depths shallower than around 19 m, descent rates are no longer affected by positive buoyancy.

In chapter 1, it was concluded that type 2 dives may reflect searching behaviour, whereby turtles can scan the water column during the deeper excursions (deeper than the gradual ascent). According to the present study, turtles are most likely to be negatively buoyant during the deeper excursion of type 2 dives, and the associated descent rates probably result from the searching behaviour, before the turtle ‘bounces’ back up to start the gradual ascent phase.

Descent and ascent tactics

Several studies have investigated the influence of changes in buoyancy underwater on the associated rates of vertical movement. For instance, mean descent rates of Elephant seals were significantly correlated with their body buoyancy, with less buoyant individuals (relatively low body-fat content) drifting deeper faster than seals with an artificially increased buoyancy (Webb *et al.* 1998). A fundamental study compared modelled and recorded vertical movements of diving guillemots (Lovvorn *et al.* 1999). These birds regulated their descent speeds in order to optimise physiological and mechanical efficiencies with regards to changes in buoyancy (due to the compression of air spaces). They were found, however, to maintain an overall constant descent speed (rather than changing speed as buoyancy changes), the speed being contained within a range minimising the drag coefficient. Consistent with one prediction made in the introduction, it was found in the present study that Green turtles descend at rates that change in the same way that their buoyancy is modelled to be changing (through lung compression with depth). Such diving tactic, which was consistently followed by the five individuals, appear to be dictated by mass-specific lung volumes (used as an indicator of the intensity of up-thrust). Their ascent tactics are less clear than the descent tactic, suggesting that the energetic implications of up-thrust on descent are more critical than those on ascent.

The descent tactic

The literature is rich in examples of adaptive behaviours, aimed at overcoming the energetic hurdle created by high positive buoyancy upon leaving the surface. For instance, juvenile Hawksbill sea turtles descend immediately following the last inspiration, submerging head first and using powerful flipper strokes on a steep descent path (hence reflecting a rather vigorous submergence effort; van Dam & Diez 1997). Their descent tactic is very consistent with those recorded in the present study, with a clear deceleration of descending movement with increasing hydrostatic pressure. During vertical dives, leatherback turtles were found to initiate each dive with a bout of high-speed swimming that gradually slowed with increasing depth (Eckert 2002). It was suggested that the high speed swimming at the beginning of the dive reflects an effort to overcome the effects of positive buoyancy but, as the lungs compress, the turtle becomes able to glide to the maximum depth of the dive with reduced energy expenditure. Similarly, rapid increases of descent speed were associated with the beginning of each descent for diving Blue Marlin, *Makaira nigricans*, which possess an unusual swim bladder (Block *et al.* 1992). The authors suggested that this initial increase in descent speed was a consequence of the difficulties in getting a positively buoyant fish away from the surface. Even though descent rates upon leaving the surface are not always reported in the literature, the powerful stroking recorded during the initial descent in the high buoyancy zone for Bottlenose dolphins, Adélie penguins (*Pygoscelis adeliae*), King penguins (*Aptenodytes patagonicus*), and North Atlantic Right whales are most probably associated with relatively fast descent rates (Williams *et al.* 1999, Nowacek *et al.* 2001, Sato *et al.* 2002). Such vigorous stroking strongly suggests hard work against positive buoyancy at shallow depth. In addition, faster swim speeds and/or descent rates upon leaving the surface have not been observed in other aquatic animals such as sharks (Block *et al.* 1992), possibly because they are negatively buoyant at all depths (Bone & Roberts 1969).

There are two ways of explaining the descent tactic recorded in the present study. Descending faster in the high buoyancy zone upon leaving the surface makes sense if the tactic is to reduce transit costs by minimising the proportion of time spent in the depth zone where up-thrust is greatest. Alternatively, the fast descent rates recorded at the start of dives may reflect the turtles trying to build up momentum to overcome buoyancy resistance. They have a large mass, so if they can build up some momentum it would be helpful in overcoming positive buoyancy near the surface. Diving ducks leap upwards in an arched dive when they initially submerge (Wilson *et al.* 1992), hence using the kinetic energy derived from a plunge for the same reasons. Turtles cannot plunge so to reach, quasi-instantly, fast descent rates in the high buoyancy zone. Instead, there may be an acceleration phase before turtles reach adequately fast descent rates, and can build up momentum. This physical restriction applied on the submergence of turtles may have limited the magnitude of descent rates upon submerging: this is suggested by the presence of a plateau value, and even slightly slower descent rates during the initial descent (at 0 – 20% of maximum depth, see figure 2-2 A-E, p. 88).

Ascent tactic

During the ascent of type 1 and 2 dives, rates of ascent accelerated, presumably in line with lung expansion, the declining depth and declining hydrostatic pressure. Based on a rapid visual observation of the recorded patterns of ascent, the acceleration appeared to be linear until shortly before the turtles broke the surface, when ascent rates tended to be slower. Bottlenose whales also decelerate slightly during the final ascent (around 250 m) of deep dives (> 850 m), but the authors (Hooker & Baird 1999) believe that this deceleration aims at reducing the rate at which gas bubbles appear in the blood and tissues of this deep diver (hence minimising the risk of nitrogen narcosis). The same physiological reason was put forward to explain why Adélie and King penguins use shallower ascent angles and slow down upon breaking the surface (Sato *et al.* 2002).

Meanwhile, the shallow-diving Hawksbill turtle (van Dam & Diez 1997) presents a more similar re-surfacing behaviour to the Green turtles of the present study, with ascending movement accelerating gradually until shortly before breaking the surface at very shallow angles. In contrast, for Leatherback turtles performing vertical dives, there was a gradual increase in the swim speed during ascent, probably as a result of positive buoyancy (Eckert 2002).

Green turtles may be capable of ascending passively, by using the buoyant lift of their lungs (Glen *et al.* 2001). Lung expansion being exponential (Boyle's Law), one might predict that ascending movement should show an exponential acceleration. In the present study, the acceleration of ascent rates with decreasing depths seemed to remain linear, and this may result from two factor (and maybe a combination of both). Firstly, if the posture of the animal during ascent is rather horizontal (as suggested in above citation), this may dramatically increase the value of the hydrodynamic drag, acting to prevent ascending movement. Secondly, the angle of ascent may switch to become rather shallow upon reaching the surface (similarly to Hawksbill turtles, see above). These two factors would explain declining ascent rates upon re-surfacing, as well as allowing the turtle to scan its surroundings for potential threats (i.e. reflecting vigilance). Right whales, which naturally do not show such predator avoidance behaviour (i.e. slowing down their final ascent) have, as a result, comparatively greater risks of vessel collision upon surfacing (Nowacek *et al.* 2001).

Diving guillemots (Lovvorn *et al.* 1999) also show a gradual increase in ascent rates with decreasing depth at small positive buoyancies, and ascent may be mostly passive via up-thrust. The observed ascent rates of these birds were, however, greater than with buoyancy alone, indicating that there was some locomotor activity superimposed on the static lift nearer to the surface. Another example of powered ascent is the final ascent to the surface by dolphins, which often showed active stroking with periods of gliding using the buoyant lift of their lungs (Williams *et al.* 1999).

The present study only reveals that ascent may involve some locomotor action superimposed onto passive upward gliding *via* positive buoyancy, but irrespective of whether ascent is entirely passive or 'powered', the energetic savings could nevertheless be considerable. For instance, passive locomotion aided by changes in positive or negative buoyancy with depth can provide up to 60% reduction in the energetic cost of diving by Weddell seals (*Leptonychotes weddellii*, Williams *et al.* 2000). Divers, such as the Northern Elephant seal, the Bottlenose dolphin, the North Atlantic Right whale, and the Blue whale (*Balaenoptera musculus*) may also reduce energy expenditure and extend dive duration, through the use of such glide patterns as part of a cost efficient locomotor tactic (Williams *et al.* 2000, Davis *et al.* 2001, Nowacek *et al.* 2001). A Partly passive ascent, as shown by the absence of flipper beating upon reaching the surface, has been reported for Adélie and King penguins, and gliding movement was attributed to increased buoyant lift due to the expanding air volumes in the body (Sato *et al.* 2002).

In conclusion, the present study gives new insights into the physical and behavioural factors that may dictate the descent and ascent behaviours of diving Green turtles. Detailed measurements of short-term changes with depth of rates of vertical movement match predictions of fast rates in the high buoyancy zone, and rates progressively slowing down when up-thrust declines. The finely tuned descent and ascent tactics of this species, during mid-water diving, may have far-reaching consequences on how shallow-divers in general live their lives in the context of changes in buoyancy with depth. The extensive use of such descent and ascent tactics are a key part of the behavioural ecology of Green turtles, and are predicted to lead to an optimal utilisation of energy resources whilst diving. Moreover, as Green turtles perform these dives during long-distance travel (Hays *et al.* 2001a and chapter 1), these energy-saving diving patterns increase the likelihood of surviving such long trips across the open oceans.

CHAPTER 3

Diving behaviour of inter-nesting Green turtles at Ascension Island

INTRODUCTION

The population of Green turtles, breeding and nesting at Ascension Island (mid-Atlantic), has been the subject of numerous scientific studies over the past decades (e.g. Koch *et al.* 1969, Carr & Coleman 1974, Carr *et al.* 1974, Mortimer & Carr 1987, Mortimer & Portier 1989). Aspects of their biology that have been examined more recently include nesting activity (Godley *et al.* 2001), nest site selection (Hays *et al.* 1995), temperature-dependent sex ratios (Broderick *et al.* 2001, Godley *et al.* 2002b), reproductive investment (Hays *et al.* 1993, Godley at al. 2001a), fasting and body size (Hays *et al.* 2002a), post-nesting migratory routes (Luschi *et al.* 1998, Hays *et al.* 2002b), diving behaviour (Hays *et al.* 2000a, 2001a), navigational abilities and orientation (Papi *et al.* 2000, Luschi *et al.* 2001). Both male and female Green turtles are thought to migrate from their feeding grounds off the coast of Brazil to Ascension Island, where they reproduce, before heading back to Brazil at the end of the nesting season. During the stay at Ascension Island, pressure data loggers have shown that adult female spend extended periods of time on the sea bed, performing what are thought to be resting dives (Hays *et al.* 2000a). There is also some evidence, obtained from satellite telemetry and short-term tracking experiments (e.g. using buoys), that adult females carry out spatially restricted movements close to the island, with turtles possibly remaining quite close to the beach where they tend to lay their eggs (Mortimer & Portier 1989, Hays *et al.* 1999).

Although tracking studies do not provide pressure measurements, it is possible to interpret some aspects of diving from the bathymetry of the area, or from submergence information (mainly mean dive durations, e.g. Renaud & Carpenter 1994, Hughes *et al.* 1998, Hays *et al.* 2001c). Similarly, although studies using pressure data loggers, such as Time-Depth-Recorders (TDRs), provide very precise and informative dive profiles, they crucially lack information on horizontal movements (e.g. Houghton *et al.* 2002) and, above all, the logging devices need to be recovered in order to download the information they contain. Some satellite tracking units, called Satellite-Linked-Time-Depth-Recorders (or SL-TDRs), however, include pressure sensors from which a limited amount of diving information can be derived (e.g. Burns & Castellini 1998). In effect, the Argos location system (Argos 1996) only allows messages of a certain length to be transmitted (and at a given frequency) to over-passing satellites:

therefore the pressure information must be compressed to fit with the limitations of Argos. Pressure information, for example, may be collected continuously over periods of a few hours (usually 6 h), and then compressed into depth histograms, before being transmitted to over-passing satellites (e.g. Godley *et al.* 2002c). There is much speculation, however, when it comes to analysing and interpreting compressed diving information, since similar summary values (e.g. mean dive duration, mean dive depth) can be generated from very disparate diving behaviours.

To overcome this problem, researchers at the Sea Mammal Research Unit (SMRU, St Andrews, UK) have designed a Satellite Relay Data Logger (or SRDL) where the micro-processor is capable of compressing pressure information into a format that allows the subsequent re-construction of individual dive profiles. Because much information has been gathered over the past years on the diving behaviour of Green turtles during their inter-nesting period at Ascension Island, it was thought to be very informative to compare the data obtained from these SRDLs with data previously collected from TDRs studies, tracking experiments and satellite telemetry.

No previous study simultaneously collected location, pressure and swim speed information, as a result of which some aspects of the behaviour of Green turtles at Ascension Island have been obtained indirectly. For instance, the relatively long dives performed by adult females on the sea bed are thought to be resting dives. The water surface is known to represent a dangerous zone where to stay because the ‘silhouette effect’ makes animals more detectable from below by potential visual predators, such as sharks (Denton 1971, Campagna *et al.* 1995, Crocker *et al.* 1997, Campagna *et al.* 2000, Le Boeuf *et al.* 2000, Gordos *et al.* 2003). Hence, if Green turtles of Ascension were to rest, they would be predicted to do so away from the water surface, e.g. on the sea bed. One reason why these long dives on the sea bed are thought to be resting dives, rather than foraging dives, is that there are no sea grasses and macro algae around Ascension Island (Carr *et al.* 1974, Mortimer & Carr 1987) for this benthic herbivore to feed on (Bjorndal 1980). In addition, stomach content analyses have revealed that the guts contained no ingesta (Hays *et al.* 2002a). In Cyprus, where such foraging material is widely found on the sea bed, Green turtles have been shown to perform both foraging and resting dives on the sea bed (Hochscheid *et al.* 1999). Heithaus *et al.* (2002) have, however, recently demonstrated (using animal-borne video cameras) that Green turtles also consume scyphozoans, but even if turtles in Ascension were feeding on scyphozoans, this would be unlikely to take place during dives to the sea bed. There has been, meanwhile, no direct evidence as yet (except some observations by divers, e.g. Hays *et al.* 2002c) that turtles remain stationary on the sea bed, i.e. behaviours involving horizontal swimming and/or constant rubbing at constant depth would generate similar U-shaped dive profiles.

In this study, SRDLs from the SMRU were used for the first time on freely diving marine turtles. Using the pressure, location and swim speed information obtained *via* satellite telemetry, it was attempted to confirm some of the direct and indirect results reported in previous studies, namely the depth utilisations, the locations of inter-nesting turtles and the actual function of the dives to the sea bed. A model, previously developed to estimate how oxygen stores vary with the depth at which turtles achieve neutral buoyancy, was adapted to further investigate the positive relationship existing between duration and depth during dives to the sea bed. In short, shallow-diving sea turtles, such as Green and Loggerhead turtles are thought capable of adjusting the volume of air they inhale prior to submerging, in order to become, through lung compression, neutrally buoyant at depth (Milsom 1975, Minamikawa *et al.* 1997, Hays *et al.* 2000a, 2001a). For mid-water dives, during which buoyancy was changed experimentally, the selection of the depth of neutral buoyancy was shown to be passive (Minamikawa *et al.* 2000). For Green turtles at Ascension Island, being neutrally buoyant whilst on the sea bed would allow them to remain passively on the sea bed, without having to expend energy to counteract buoyancy forces (being too negatively buoyant on the sea bed would require to expend more energy for the subsequent ascending movement). Since greater lung volumes upon submerging are associated with deeper depths at which neutral buoyancy is attained, the associated greater oxygen stores contained in the lungs (which are the main oxygen store for shallow-diving turtles such as the Green, Loggerhead and Hawksbill turtles; Lutz & Bentley 1985, Lutcavage & Lutz 1997) will permit longer dive durations. In the present study, it was attempted to model the durations of dives to given depths by building boundary lines, which are predicted to better describe and explain the positive relationship that exists between dive duration, oxygen stores and diving metabolic rate.

MATERIALS & METHODS

Fieldwork

Fieldwork was conducted on Ascension Island in June 2001. Satellite transmitters were attached to four female Green turtles nesting on Long Beach (for detailed information about the attachment procedure, see Hays *et al.* 2002b). Briefly, each turtle was approached when egg laying had finished to minimise disturbance. The carapace was quickly wiped with acetone (to remove any grease), then lightly cleaned with a mildly abrasive sandpaper, and finally wiped again with acetone. The units were then glued onto the carapace using a quick setting two-component epoxy resin (Foilfast, SFS Stadler, Cheltenham, U.K.). The attachment procedure lasted no more than 20 minutes, and turtles were left to finish covering their nest before returning to the sea.

Satellite transmitters

The satellite transmitters, manufactured by the Sea Mammal Research Unit (SMRU, St Andrews, U.K.) were originally designed for the study of seals, which are likely to damage instrumentation by rolling when on land. The robust design of these units minimised the risk of damage caused by turtles during the inter-nesting period. The units were series 7000 Satellite Relay Data Loggers (McConnell *et al.* 1999), which were equipped with several sensors, such as a pressure sensor, a submergence sensor (or salt-switch-salt, SWS) and a swim-speed sensor. The SWS is a device that allows the micro-processor to detect whether the SRDL is underwater and transmissions are blocked when the unit is underwater, increasing battery life. The on-board micro-processor collected the values read by the sensors, and summarised/compressed this information into 256-bit messages (Fedak *et al.* 2001, 2002).

Messages were transmitted as uplinks as soon as the SWS detected the animal at the surface. The transmission frequency was specified by the Argos system, with a maximum of one transmission per 40 seconds. The most recent messages were given priority over older messages, and messages could be transmitted and received by a satellite more than once. If transmission was not possible for long periods of time, the memory of the SRDL may have become saturated, and the oldest messages over-written by newer data.

Satellite locations and speed of horizontal movement

Satellite locations were selected and analysed as described in the Materials & Methods in chapter 1 (p. 38). Movements of inter-nesting turtles at Ascension Island are known to be of relatively small scale. Therefore, in order to estimate the horizontal distances between pairs of locations, it was sufficient to use Pythagoras's theorem instead of more rigorous formulae for great circle calculation. The horizontal distance equivalent to one degree of latitude (or one degree of longitude, since these distances should be comparable at the latitude of Ascension Island) was calculated using the standard formula for great circle calculation. Hence, one degree of latitude (or longitude) was approximately equivalent to a distance of 110.55 km; applying Pythagoras' theorem, the distance (in km) between locations A and B was:

$$\text{Distance} = \surd \{ [(\text{Lat}_B - \text{Lat}_A) \times 110.55]^2 + [(\text{Lon}_B - \text{Lon}_A) \times 110.55]^2 \}$$

The speed of horizontal movement (in km/h) between two successive locations was then calculated as the ratio of the horizontal distance travelled by the amount of time elapsed. In order to calculate the mean position of each individual's inter-nesting range, at least 50% of the locations for each turtle were used, retaining the cluster of locations that were closest to each other, i.e. those locations that minimised the total inter-sample distance (Hays *et al.* 1999).

Compression of pressure information

A submergence was considered a dive when a pressure measurement corresponding to a depth of 6 m was obtained (i.e. submergences remaining shallower than 6 m were not classed as dives). Water pressure was read every second (to the closest 10 cm) by the microprocessor, which then selected the five time-depth points of the dive profile where trajectories changed most rapidly (Fedak *et al.* 2001). These points were referred to as the 'greatest inflection points' of the dive (figure 3-1 A, p. 98). During the course of a dive, if one of the greatest inflection points occurred between 0 and 6 m below the surface, the micro-processor encoded it as 0 m. Dive duration ('Dur', in seconds) was calculated by the micro-processor using the SWS.

Using (1) the times at which the five inflection points occurred during a dive (their temporal positions are given as a percentage of dive duration, P1 to P5) and (2) their corresponding depths (D1 to D5), dive profiles could be reconstructed. To build

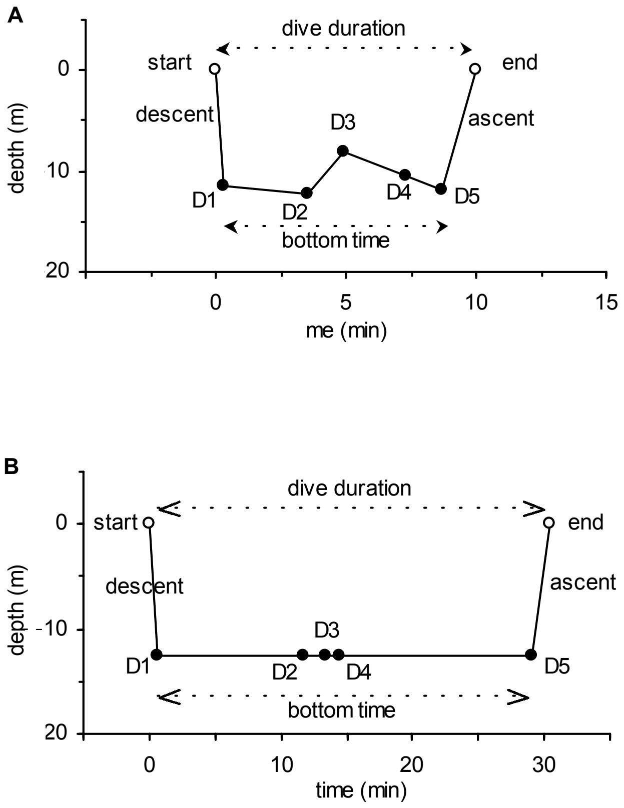


Figure 3-1. (A) A typical example of a dive, the profile of which was built from the pressure information provided from the SRDLs. The points D1 to D5 are the five major inflection points. The dive duration and bottom times are shown. (B) A typical example of a U-shaped dive (turtle 1), for which the five inflection points were usually located on the sea bed.

dive profiles, the relative times at which the five greatest inflection points occurred (P1 to P5) were transformed into 'real' time (T1 to T5). For example, the first major point of inflection of a dive (described as D1/P1) occurred at T1 = (P1 x 100) / Dur. Any dive was described by a total of seven points:

- Point 1: the point at which the dive started was at t = 0 sec and at depth D0 = 0 m.
- Points 2, 3, 4, 5, 6: the five major inflection points were at t = T1 to T5 and at depths D1 to D5.
- Point 7: the point at which the dive ended was at t = 'dur' sec and at depth D7 = 0 m.

The bottom time of a dive was defined as the amount of time elapsed between the second (T1; D1) and sixth (T5; D5) points describing the dive (figure 3-1 A, p. 98).

Discrimination of U-shaped dives from other dives

Inter-nesting turtles, at Ascension Island, are known to spend a considerable proportion of their time on the sea bed. In the dive record, this behaviour was seen as U-shaped profiles (e.g. figure 3-1 B, p. 98; Hays *et al.* 2000a), during which, little time was spent moving from the surface to the sea bed (and back), and most of the dive duration was spent on the sea bed. It was possible to differentiate between U-shaped dives and other dives in an automated fashion, employing user-defined macros. The macros selected dives during which more than 85% of the dive duration was spent within 2 m of the maximum depth of that dive. The set of selected U-shaped dives was then double-checked, visually, by running another macro plotting the time-depth profile of each dive.

Swim speeds during a dive

The speed sensor assessed the speed of the swimming turtle by measuring the rotation speed of its internal paddle-wheel turbine (the stall speed is calibrated by the manufacturer and equals 0.05 m s^{-1}). Using the values provided by the speed sensor, the microprocessor calculated the mean swim speeds (in m s^{-1}) during:

- the descent portion of the dive (S_D, between the surface and D1),
- the bottom portion of the dive (S_B, between D1 and D5),
- the ascent portion of the dive (S_A, between D5 and the surface).

The actual distance swam during each of the phases of a given dive (descent, bottom and ascent phases) was calculated by multiplying the swim speed during a phase by the duration of that phase, both parameters being provided by the micro-processor. The mean swim speed during an entire dive was calculated as the sum of the distances covered during the three phases of the dive (descent, bottom and ascent), divided by the dive duration.

RESULTS

Satellite information and movements during the inter-nesting period

Satellite locations were obtained for five inter-nesting periods (turtle 1 nested twice), before the four tracked turtles eventually left the island, heading back to Brazil (tracks in Hays *et al.* 2002b). Nesting events were either confirmed by direct visual observation (i.e. during a night patrol), or when one or more locations of high accuracy (i.e. location classes 3, 2 & 1, location 3 being the greatest accuracy, Hays *et al.* 2001b) were obtained. Indeed, location accuracy increases with the number of uplinks received by the over-passing satellite (see Materials & Methods in chapter 1, p. 38 and Hays *et al.* 2001b), and therefore increased accuracies of locations were usually associated with nesting events on the beaches.

The mean number of locations obtained per day varied between 1.6 and 3 (table 3-1, p. 101). For all individuals, some of the locations calculated by Argos were discarded either because they were obviously wrong (i.e. hundreds of kilometres out) or because they inferred unrealistic travelling speeds (i.e. travelling speeds > 5 km/h). At least 73% of the satellite locations of each individual were kept for subsequent analysis, with the proportion of relatively high accuracy (i.e. location classes 1, 2 & 3) varying between 7 and 20% of the total number of locations received (table 3-1, p. 101). The relatively low daily numbers of locations and the prevalence of low accuracy locations (i.e. 0, A & B, Hays *et al.* 2001b) was due to a combination of high levels of submergence by the turtles and infrequent satellite overpasses at the latitude of Ascension Island (i.e. 2 hours of coverage per day in equatorial regions, compared to up to 6 hours per day in polar regions; Burns & Castellini 1998). Because the number of uplinks received by over-passing satellites were limited by these two factors, there were

Turtle	*N* of locations per day	% of locations kept	% of LC 3, 2 & 1
1	1.6	72.9 %	8.0 %
2	1.8	78.5 %	7.1 %
3	3.0	86.0 %	18.6 %
4	2.1	92.3 %	19.2 %

Table 3-1. Number (*N*) of satellite locations received for each turtle during their inter-nesting periods; proportion of locations kept for subsequent analysis; percentage of location classes (LC) 1, 2 & 3 within the full satellite dataset.

temporal gaps within the dive record of each individual, making it difficult to investigate temporal patterns in diving behaviour.

Because most of the satellite locations were of low accuracy (mainly 0, A & B), it was not possible to resolve any route that may have been followed by the inter-nesting turtles. It was, however, clear that the four tracked turtles did not travel significantly far from the island (figure 3-2 A-D, p. 103), rather appearing to have remained in an area just off Long Beach (where the satellite tracking units were attached). The mean positions of each individual during their respective inter-nesting periods were located in an area where the depth of the water ranged from 10 to 25 m (figure 3-3 A-D, p. 104).

Pressure information

A total number of 531 dives were obtained for the four individuals (table 3-2, p. 105). For relatively shallow dives (i.e. maximum depth around 6 m), it is likely that some of the major inflection points of the dive profiles actually occurred between the surface and 6 m, which then appeared as a surface point (i.e. depth = 0 m) in the dive record (e.g. figure 3-4 A & B, p. 106). Such relatively shallow dives were not included in the analysis.

The SWS device performed poorly in detecting the relatively short surface intervals of inter-nesting Green turtles. In effect, the start and end points of some dives appeared to have been ‘missed’ in the dive records (e.g. figure 3-4 C & D, p. 106). In theory, it was possible to overcome this problem by manually correcting the start and/or end points of dives clearly deeper than 6 m (in which case the dive duration was re-calculated). Such corrections were only performed on U-shaped dives, because their very conserved shape made the correction relatively safe. The number of U-shaped dives that had to be manually corrected (table 3-3, p. 105) represented less than 15% of the total number of U-shaped dives for each individual.

For one individual (turtle 1), it was found that some dive profiles showed two U-shaped dives, one following the next (figure 3-4 E, p. 106 and table 3-3, p. 105). This was probably due to the fact that the SWS did not detect the surfacing event between two successive U-shaped dives. These two U-shaped dives were manually separated and reconstructed, and their approximate durations re-calculated.

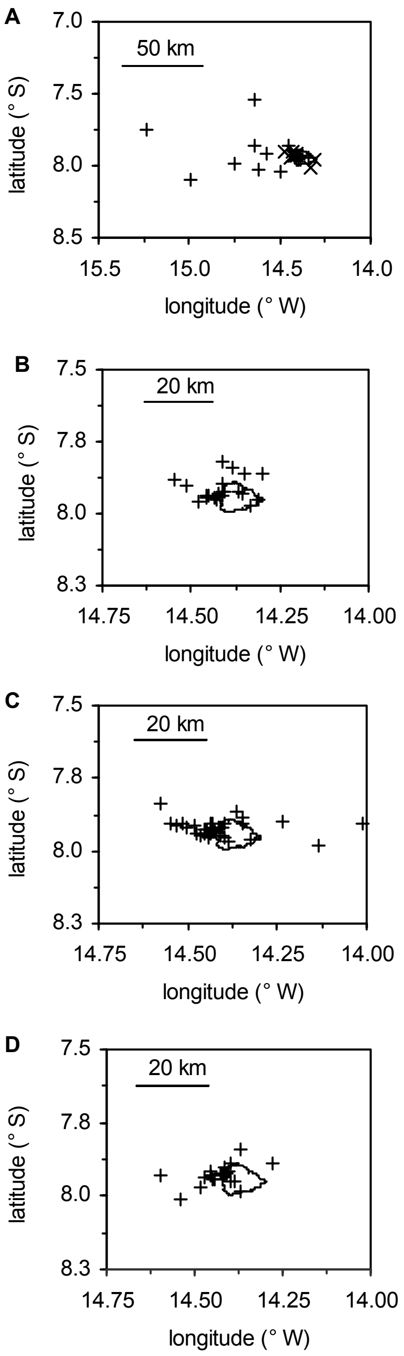


Figure 3-2. The satellite locations obtained from the four tracked turtles, during their inter-nesting periods. A, B, C & D are for turtles 1, 2, 3 & 4, respectively. For turtle 1: the first inter-nesting period is shown with +, whilst the second is shown with ×, and note the different scale.

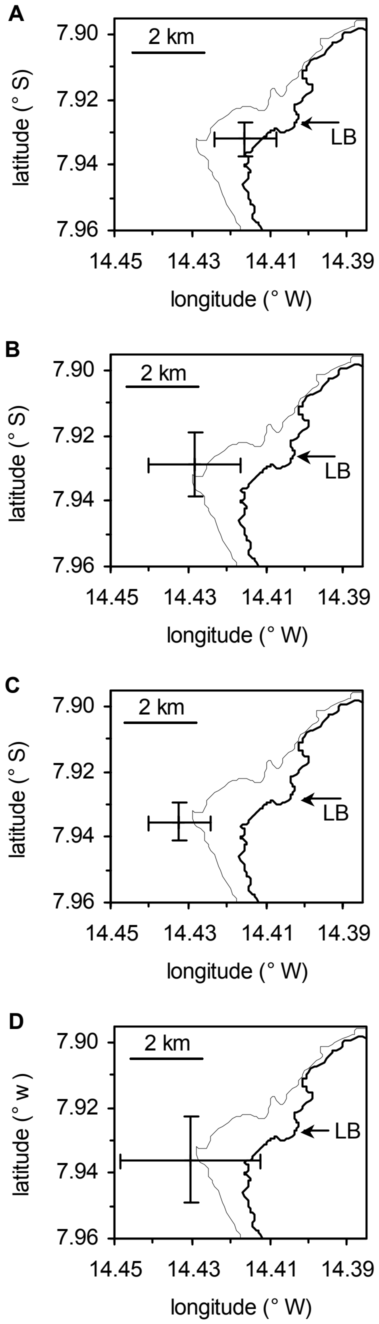


Figure 3-3. Mean positions of each turtle during their inter-nesting periods (the error bars show two standard errors to the mean position). A, B, C & D are for turtles 1, 2, 3 & 4, respectively. The 20 m depth contour is shown, as well as Long Beach (LB).

Turtle	SL-TDRs	IP (days)	*N* dives transmitted	*N* U dives	*N* non-U dives	Unclassified dives
1	4395	11 12	133	78	30	25
2	15119	15	173	98	50	25
3	15122	14	140	74	25	41
4	15120	12	85	48	20	17

Table 3-2. Satellite tracking units (SL-TDRs); durations of the inter-nesting periods (IP); number (*N*) of dives transmitted (U dives, non-U dives and unclassified dives).

U dives	Turtle 1	Turtle 2	Turtle 3	Turtle 4
N	78	98	74	48
Missed start or end points percentage:	10 13%	4 4%	7 9%	3 6%
Two U-shaped dives unresolved percentage:	8 10%	0 n/a	0 n/a	0 n/a

Table 3-3. Number (and proportion) of U dives for which the start (or the end) was 'missed' (refer to text and figure 3-4 C & D, p. 106), or for which the surface interval between two successive U dives was 'missed' (refer to text and figure 3-4 E, p. 106).

U dives	Turtle 1	Turtle 2	Turtle 3	Turtle 4
N	78	98	74	48
Mean duration (min)	30.9 ± 11.1	38.8 ± 9.3	49.9 ± 12.8	34.1 ± 9.5
Mean maximum depth (m)	14.6 ± 2.0	15.2 ± 3.1	16.8 ± 1.9	17.7 ± 1.5

Table 3-4. Mean durations and mean maximum depths of U dives are given ± 1 SD.

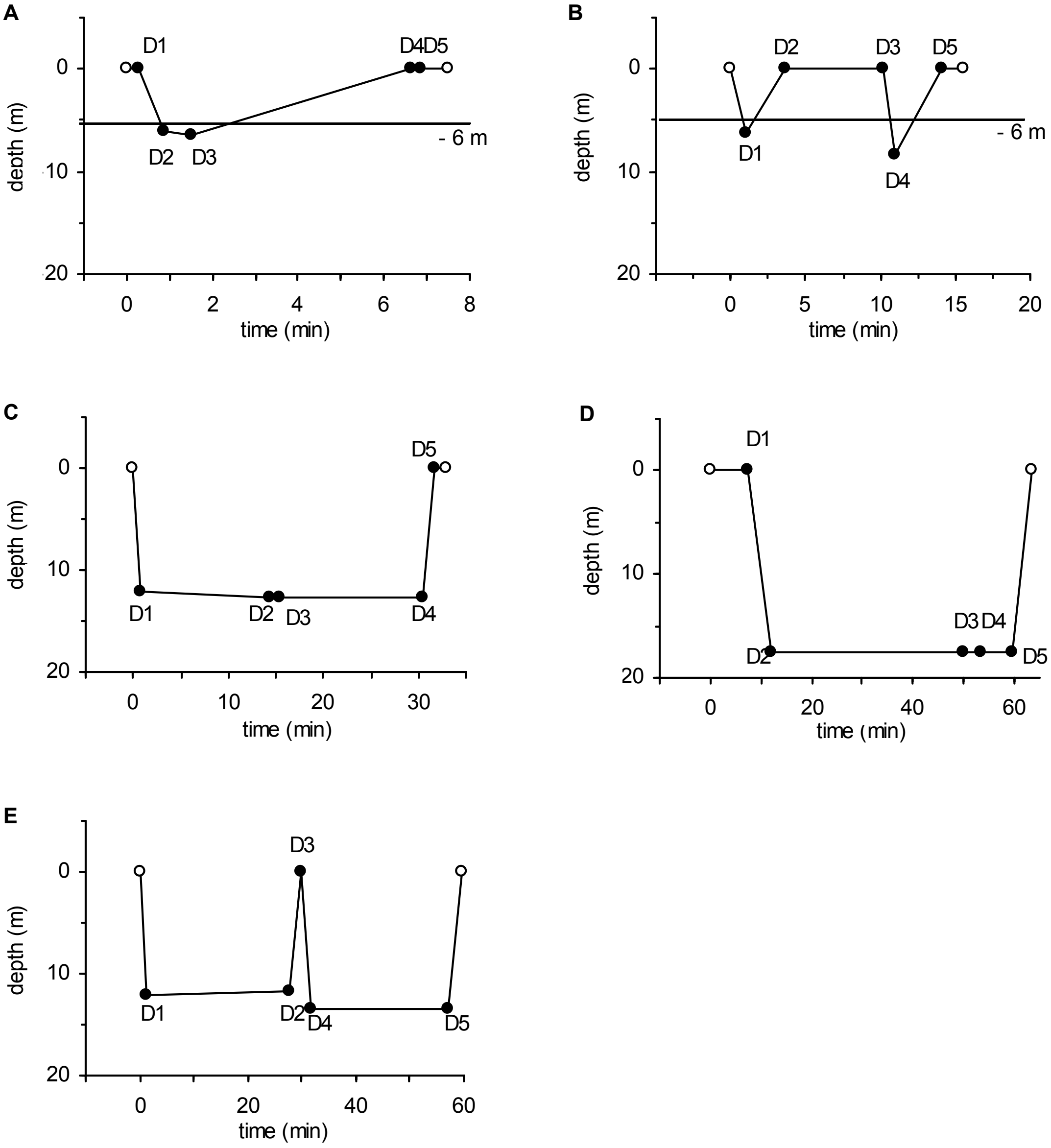


Figure 3-4. (A & B) Examples of relatively shallow dives, for which some inflection points occurred between 0 and 6 m, and hence are encoded (by the micro-processor) as occurring at the surface. (C & D) Examples of two U-shaped dives, for which the SWS device appears not to have detected the end point (figure 3-4 C) or the start point (figure 3-4 D) of the dives. (E) Example of two U-shaped dives, which were not resolved by the micro-processor, probably because the SWS device did not detect the surfacing event between these successive dives.

Diving behaviour during the inter-nesting periods

The inter-nesting periods lasted between 11 and 15 days (table 3-2, p. 105). Dives were classified into two categories: the ‘U dives’ (e.g. figure 3-1 B, p. 98) and the ‘non-U dives’ (e.g. figure 3-1 A, p. 98). This relatively basic distinction was chosen because U dives showed extremely conserved shapes, whilst this was not the case for non-U dives, which, in contrast, were extremely variable in shape both intra and inter individually.

Means durations of U dives ranged between 30.9 and 49.9 minutes (table 3-4, p. 105 and figure 3-5 A-D, p. 108), with the longest dives lasting about 63.5 minutes (turtles 3 and 4). The number of bits allocated by the micro-processor to describe the value of dive duration was insufficient to account for dives longer than 63.5 minutes; hence, it is possible that some dives actually lasted longer than 63.5 minutes. However, the frequency distributions of dive durations for all turtles (figure 3-5 A-D, p. 108) strongly indicated that dives longer than 63.5 minutes were quite rare. In contrast, the mean durations of non-U dives were significantly shorter than those of U dives (paired t-tests, $N = 4$ turtles, $t = 6.3$, $p < 0.01$). This confirms that non-U dives, whose mean durations ranged from 16.1 to 33.8 minutes (table 3-5, p. 109 and figure 3-5 A-D, p. 108), were significantly shorter than U dives.

U dives deeper than 19 m were extremely rare for all individuals (figure 3-6 A-D, p. 110), accounting for less than 10 dives over a total number of 298 U dives. Mean maximum depths for U dives ranged from 14.6 to 17.7 m (table 3-4, p. 105), and there was little variation of depth during the bottom phases of these dives (i.e. the proportion of dive duration spent between two metres of maximum depth was always > 90%). In contrast, the non-U dives showed considerable variations in depth during the bottom phase (i.e. the proportion of dive duration spent between two metres of maximum depth varied between 0 and 85%).

Mean maximum depths for non-U dives ranged between 12.6 and 18.3 m (table 3-5, p. 109 and figure 3-6 A-D, p. 110). The mean maximum depths for non-U dives were significantly less than those for U dives for turtles 2, 3 and 4 (paired t-tests, $N = 3$ turtles, $T = 28.0$, $p < 0.01$). This indicates that non-U dives tended to be shallower than U dives. However for turtle 1, the mean maximum depth of non-U dives (mean = 18.3 m) was greater than the one of U dives (mean = 14.2 m). This was most probably

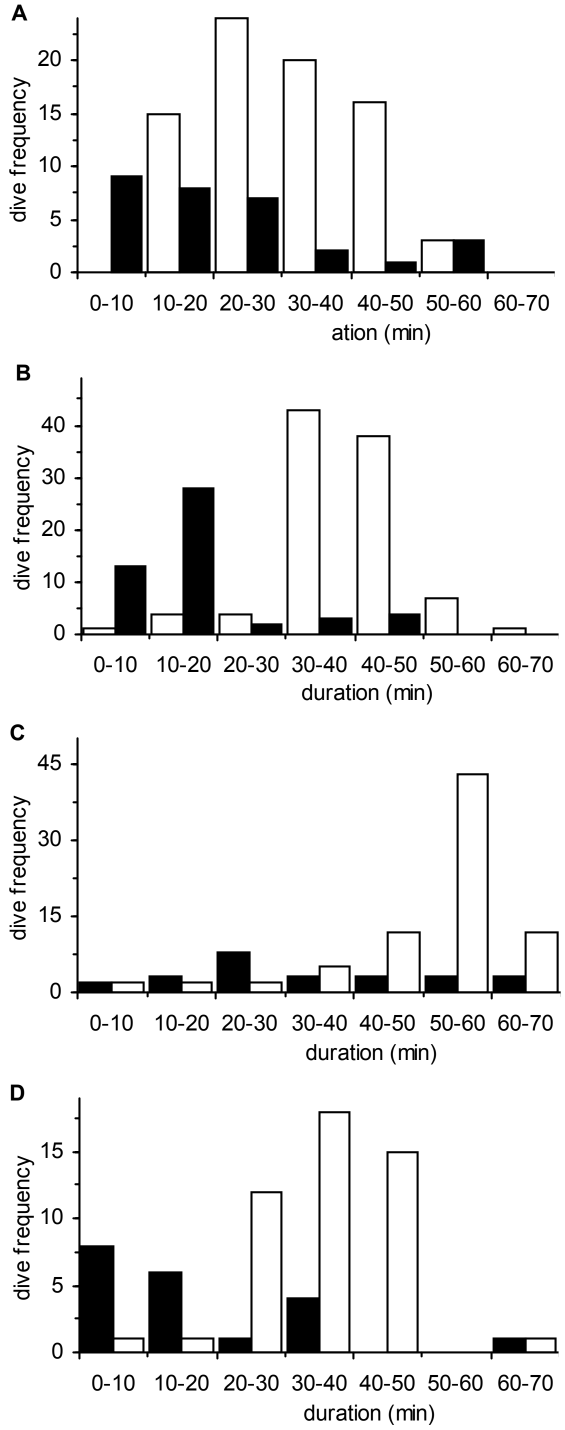


Figure 3-5. Frequency distributions of the durations of U dives (open bars) and non-U dives (solid bars), during the inter-nesting periods. A, B, C & D are for turtles 1, 2, 3 & 4, respectively.

non-U dives	Turtle 1	Turtle 2	Turtle 3	Turtle 4
N	30	50	25	20
Mean duration (min)	20.8 ± 14.7	16.1 ± 10.1	33.8 ± 17.7	18.0 ± 14.8
Mean maximum depth (m)	18.3 ± 9.7	12.6 ± 3.1	13.9 ± 3.4	14.8 ± 3.6

Table 3-5. Mean durations and mean maximum depths of non-U dives are given ± 1 SD.

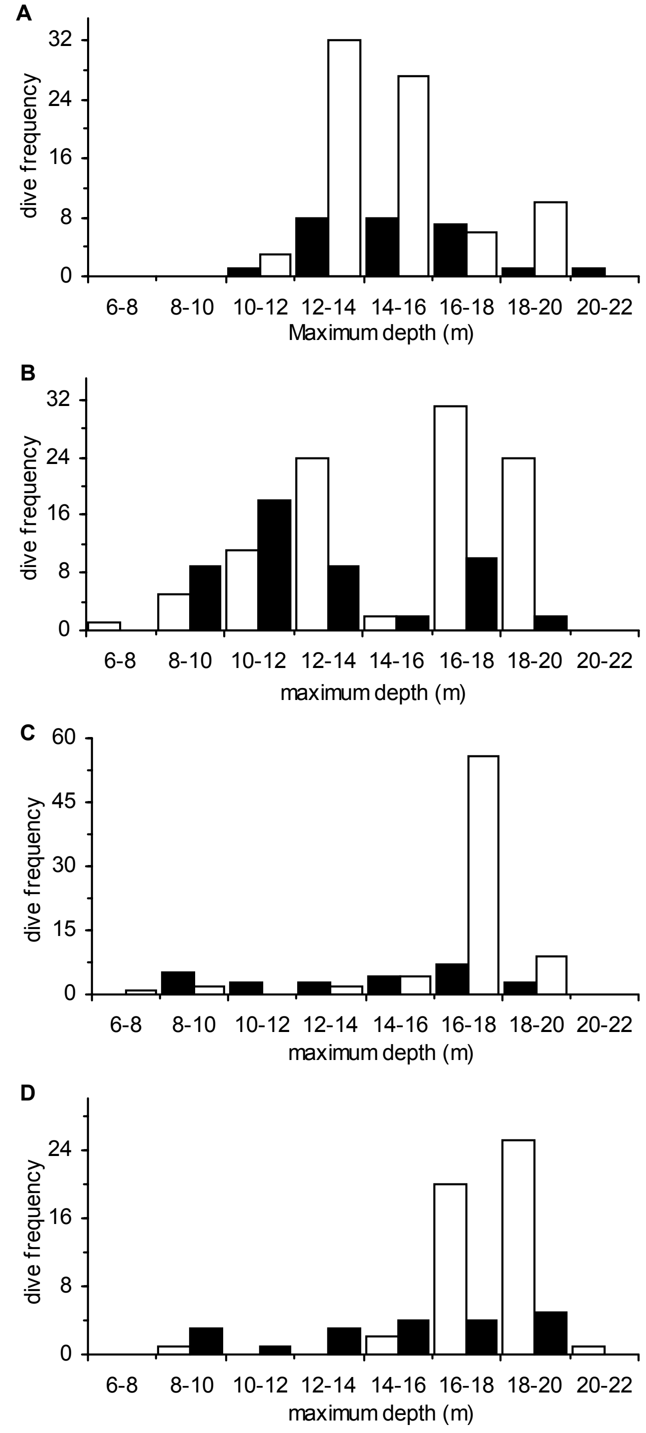


Figure 3-6. Frequency distributions of the maximum depths of U dives (open bars) and non-U dives (solid bars), during the inter-nesting periods. A, B, C & D are for turtles 1, 2, 3 & 4, respectively. For turtle 1 (figure 3-6 A), there were 4 non-U dives off scale (maximum depths: 24.0 m, 35.6 m, 40.4 m, 57.2 m).

because turtle 1 carried out some relatively deep dives during its inter-nesting period (five dives with maximum depths ranging from 20 and 60 m were recorded).

For U dives, maximum dive depths and durations appeared to be positively related (figure 3-7 A-D, p. 112). Some maximum depths, however, appeared to be under-represented (this being more the case for shallower depths (such as 6-12 m) than deeper depths) when the patterns were visually compared with data collected continuously using Time-Depth-Recorders (Hays *et al.* 2000a). When TDRs were used to record the diving behaviour during the inter-nesting intervals of two Green turtles at Ascension (Hays *et al.* 2000a), the maximum depths and durations of 259 and 165 U dives, respectively, were obtained, and all depth ranges were fairly equally represented. In comparison, the present study collected 298 U dives for a total of four turtles because diving information was collected discontinuously (*via* satellite), and this explains why all depth ranges were not represented as equally. Hence, the data for the four turtles was pooled (figure 3-7 E, p. 112) for further analysis, and it was found that the duration of U dives increased significantly when maximum depths were greater (regression analysis, N = 298 U dives by 4 Green turtles, $F_{0.05,\ 1,\ 298} = 58.7$, $r^2 = 0.16$, $p < 0.0001$). The relatively low r^2 value indicated that the scatters around the regression lines was considerable. In contrast, there was no obvious relationship between the maximum depths and durations of non-U dives.

Aspects of the resting behaviour throughout the inter-nesting intervals

Because of substantial gaps in the dive records, the data for the four turtles were pooled in order to investigate the temporal occurrence of U and non-U dives. There were clear diel patterns in the occurrences of these dives, with U dives occurring predominantly at night, and non-U dives occurring predominantly during the day (figure 3-8 A, p. 113). In contrast, maximum depths of U and non-U dives showed no clear pattern of variation with the hour of the day. There was, however, a clear variation in the daily maximum depths of U dives throughout the inter-nesting interval for turtle 2 (figure 3-8 B, p. 113). This turtle seemed to show a certain degree of fidelity to at least two sites (located at about 18 m and 13 m). The maximum depths of U dives for the other three turtles (turtles 1, 3 & 4) showed much less variability throughout their inter-nesting periods, suggesting that they probably remained in the same areas.

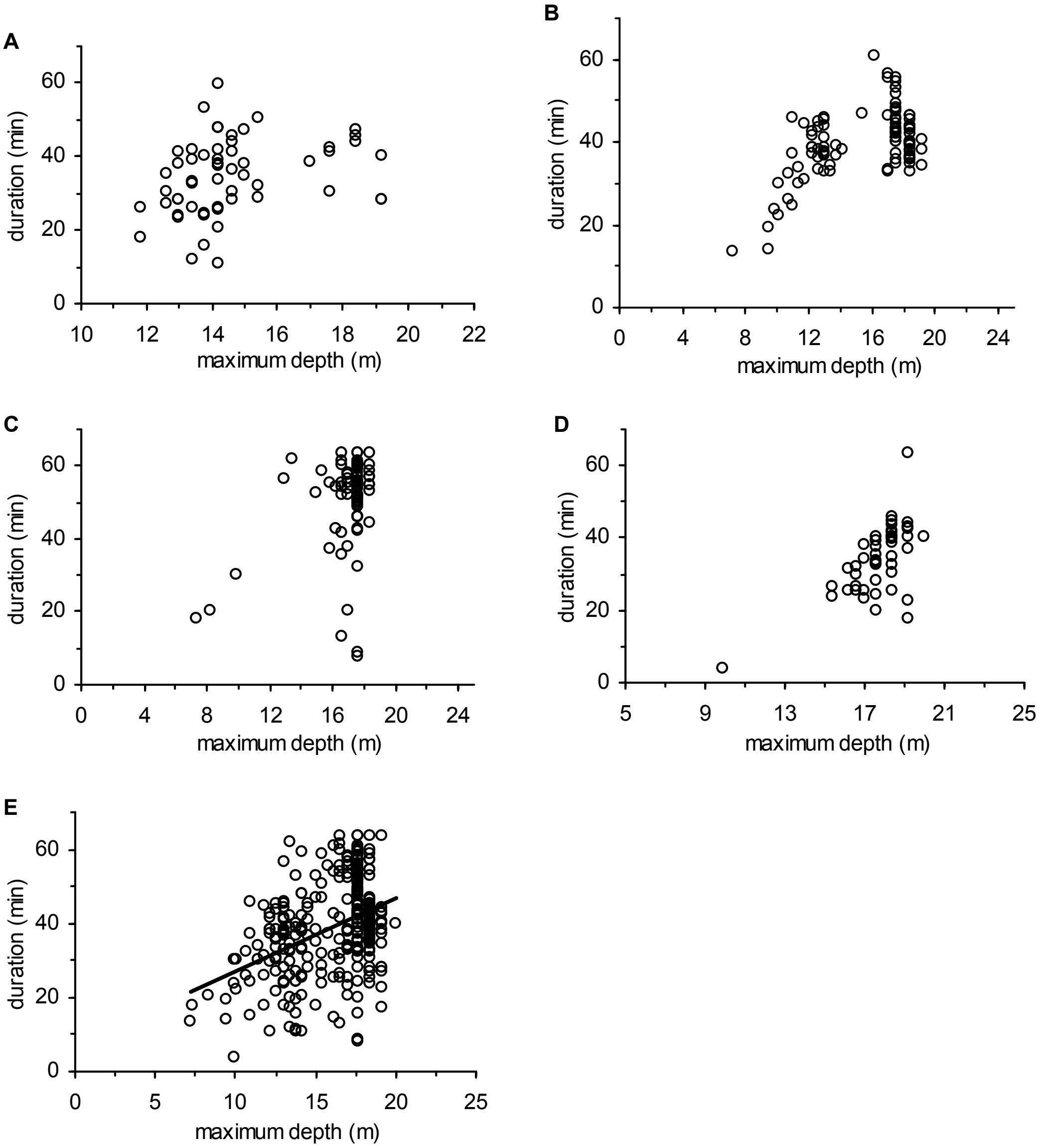


Figure 3-7. The relationship between duration and maximum depth for U dives, during the inter-nesting periods. A, B, C & D are for turtles 1, 2, 3 & 4, respectively, while E shows the pooled data for the four turtles.

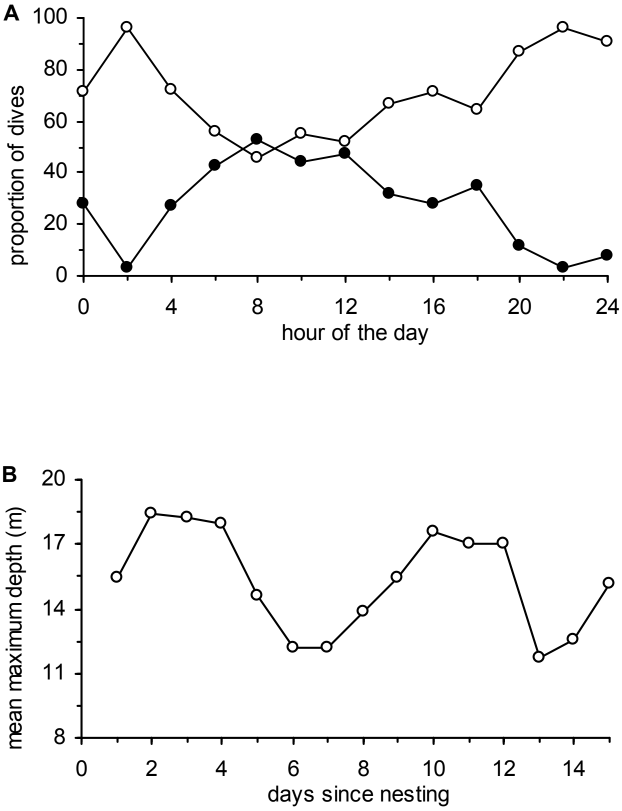


Figure 3-8. (A) Relative numbers of U dives (o) and non-U dives (•), for each 2 hour interval during the day (data for four turtles). (B) The daily maximum depths of U dives in between two nesting events (turtle 2).

Swim speed underwater (turtle 2)

The swim-speed sensor was probably the most fragile part of the SL-TDRs, since little or no data was available for three of the four inter-nesting turtles (broken sensors were confirmed for turtles 1 and 4 when they were observed re-nesting). Only one individual (turtle 2) provided a sufficient set of swim speed readings (42 of its dives had adequate data). Comparisons between rates of vertical movement and swim speeds indicated that the latter were greatly under-estimated, which may have resulted from the flow of water not entering the sensor properly, or the sensor being somehow damaged. Swim speed data for turtle 2 was consequently examined qualitatively.

During U dives ($N = 26$), the swim speed during the bottom phase was virtually nil compared to the swim speed during the descent phase, whilst the swim speed during the ascent phase was only about 20 % slower than that during the descent phase (figure 3-9 A, p. 115). In contrast, during non-U dives ($N = 16$), the swim speeds during the bottom phase and the ascent phases were only respectively 70 % and 25 % slower than during the descent phase (figure 3-9 A, p. 115).

When each phase (descent, bottom and ascent) were separately compared between U and non-U dives, it was found that the medians of the swim speeds of non-U dives (table 3-6, p. 116) during the descent, bottom and ascent were greater than the medians of swim speeds during (respectively) the descent, bottom and ascent phases of U dives (qualitative comparison). Moreover, the median of swim speeds during non-U dives, when compared to those during U dives, were about 2.7 times faster during descent and 4.5 times faster during the ascent phase (table 3-6, p. 116).

Overall, the median swim speeds over the course of non-U dives ($N = 16$, median = 0.0868 m s^{-1}) was about 14 times faster than the median of swim speeds over the course of U dives ($N = 26$, median = 0.006 m s^{-1}) (figure 3-9 B, p. 115 and table 3-6, p. 116). The fact that U dives tended to last longer than non-U dives (figure 3-9 C, p. 115, this figure shows only the U and non-U dives for which swim speed data are available) was very consistent with the fact that the overall swim speeds during U dives were slower than those during non-U dives (figure 3-9 B, p. 115). It hence seems that dives with relatively fast overall swim speeds (i.e. non-U dives) tended to be shorter than dives with relatively slower swim speeds (i.e. U dives).

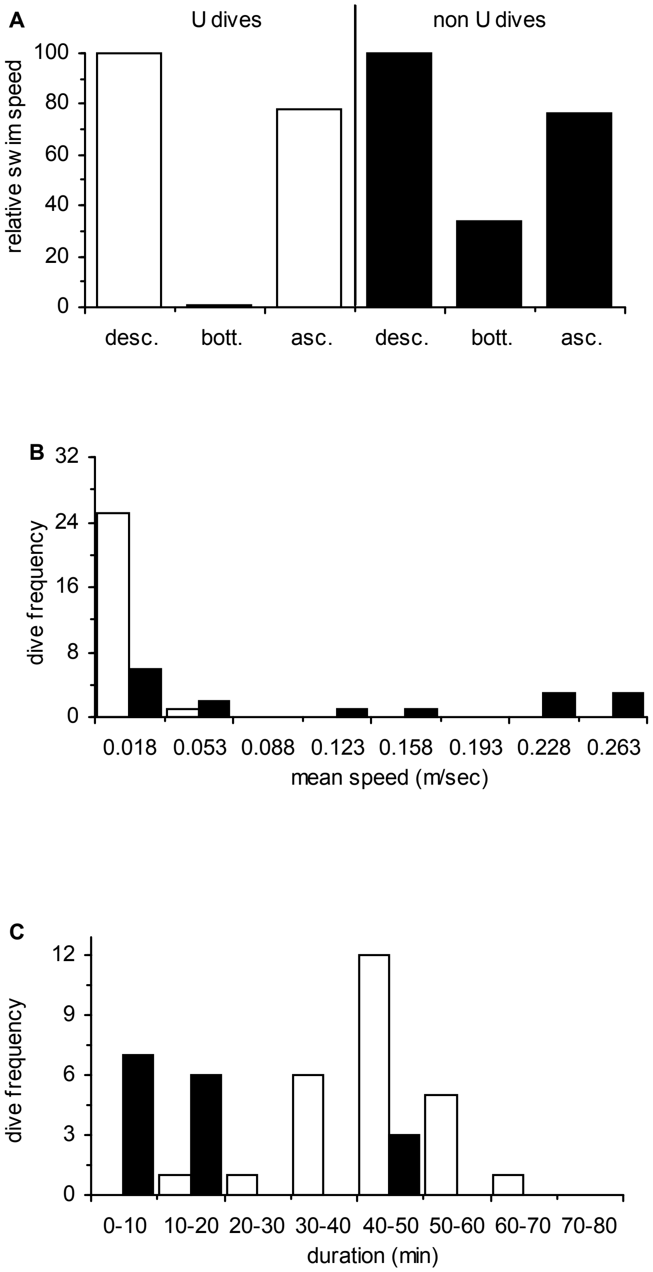


Figure 3-9. (A) For U dives (open bars) and non-U dives (solid bars), the relative swim speeds during each phases of the dives (the descent swim speed being always 100%). Descent phase is 'desc.', bottom phase is 'bott.' and ascent phase is 'asc.'. Frequency distributions of (B) mean swim speeds during the course of a dive, and of (C) the durations of these dives (see text for details).

Turtle 2	U dives	non-U dives	Ratio U/non-U
N of dives with swim speed readings	26	16	n/a
S_D (m s^{-1}) IQ range:	0.100 0.050 – 0.112	0.275 0.150 – 0.337	2.7
S_B (m s^{-1}) IQ range:	0 -	0.050 0 – 0.200	-
S_A (m s^{-1}) IQ range:	0.050 0 – 0.100	0.225 0.012 – 0.337	4.5
Speed during the dive (m s^{-1}) IQ range:	0.006 0.003 – 0.007	0.086 0.010 – 0.216	14

Table 3-6. Medians of swim speeds during the descent phase (S_D), bottom phase (S_B), ascent phase (S_A), and during the course of U and non-U dives (turtle 2). The ratios of the median swim speed of non-U dives by the one during U dives are given.

DISCUSSION

As well as the methodological advance provided by the combination of satellite and depth telemetry, the present study both confirmed the results of previous studies and provided new information on the inter-nesting behaviour of Green turtles at Ascension. Indeed, turtles tended to remain close to the beach where they had nested, while the diel pattern of occurrence and depth range of the dives to the sea bed were consistent with a previous TDRs study (Hays *et al.* 2000a). In addition, the limited speed information gave new insights into the differences in activity levels of dives to the sea bed compared to other dives. This information will be used to confirm the probable function of these dives to the sea bed.

The SRDLs used in this study were found to be rather adequate for the investigation of dives deeper than 6 m, despite substantial temporal gaps in the dataset. Nevertheless, the limited pressure information that was collected *via* satellite has appeared to be sufficient to permit acceptable interpretations of data, since the results could be compared with the more precise pressure information that had been collected in the past (using TDRs). The use of satellite and depth telemetry allowed to increase the number of individual studied as well as receiving the information directly *via* satellite telemetry since no instrumentation needed to be physically recovered.

Satellite information and movements during the inter-nesting period

The daily numbers of satellite locations obtained for the four inter-nesting females were, on average, much greater than those obtained during a previous study using Telonics satellite transmitters (0.92 locations per day, Hays *et al.* 1999). Both the present study and that earlier one mainly provided locations of relatively low accuracy. This suggests that, at similar latitudes, location accuracy is less dependent on the design and quality of specific satellite transmitters, and more dependent on the behaviour of sea turtles. Surface intervals may be just too short to allow sufficient uplinks to be transmitted to over-passing satellites, hence limiting the location classes to mostly low accuracies.

During the inter-nesting periods at Ascension Island, all four turtles remained fairly close to the beach where their satellite transmitters were attached (i.e. Long Beach), as shown by the clusters of locations obtained for each turtle. This finding was consistent with (1) the depth utilisation recorded for the inter-nesting periods (with maximum depths mostly shallower than 20 m, although turtle 1 performed some relatively deep non-U dives up to 60 m deep), and with (2) the fact that the water is not deeper than 30 m within a few kilometres around Ascension Island, whereas further offshore, the sea bed rapidly reaches depths of several hundreds of metres (see figure 1-5, p. 47).

Limited travelling movements during the inter-nesting periods were also reported in previous studies at Ascension Island, when turtles were tracked using floats attached to their carapaces with 20 m lines (Carr & Coleman 1974, Mortimer & Portier 1989) or using satellite tracking units (Hays *et al.* 1999). These studies, which had no direct pressure information, suggested that inter-nesting females did not travel significantly far from the beach where they had been observed nesting, and essentially remained in waters of depths ranging from 10 to 20 m, performing long duration dives assumed to be resting dives on the sea bed (Carr & Coleman 1974). The present study has used a combination of location and pressure information to confirm these hypotheses.

Pressure and speed information

The possible functions of non-U dives are extremely varied, including all underwater activity that does not involve sitting on the sea bed, e.g. local exploration, sub-surface travelling dives, or mating activity. Consequently, the depth utilisation during non-U dives was not expected to be constrained to given depth ranges, and these dives indeed had a relatively wider range of maximum depths. The fact that any depth reading occurring between 0 and 6 m is considered (by the micro-processor) to be at 0 m makes it impossible to investigate near surface diving behaviours, particularly for the sub-surface travelling dives located in the upper 2 m of the water column (e.g. Hochscheid *et al.* 1999, Hays *et al.* 2001a, Houghton *et al.* 2002, Eckert 2002).

Hence, non-U dives were quite sensitive to the fact that the 0 to 6 m depth range was ‘disregarded’ by the micro-processor. While U dives may not be too affected by the 0 to 6 m restriction for depth readings (since they present a narrower and deeper range of depth utilisation), it is likely that the dive record may not accurately reflect the actual occurrence and depth utilisation of non-U dives. This is one reason why non-U dives were not examined in more detail, another reason being that five inflection points makes it difficult to accurately derive the actual shapes of non-U dives from their profiles (five inflection points appear to be insufficient to describe these dives).

A total of 26 U dives and 16 non-U dives performed by turtle 2 had reliable swim speed information. Therefore, although the sensor on turtle 2 appears to have been able to record swim speeds, only a limited number of values were available. In some cases, it is possible that the turbine of the speed sensor was prevented from rotating as if some foreign material had penetrated the sensor. Moreover, the swim speed data did not have the same level of priority for transmission as, for example, pressure information did have: therefore, even if data was collected by the micro-processor, it may not have been transmitted to over-passing satellites.

Diving behaviour during the inter-nesting periods

Overall, the diving behaviour that has been obtained from satellite transmitters by the present study was consistent with the results of previous studies carried out at Ascension Island, studies which either used the pressure information derived from TDRs (Hays *et al.* 2000a) or the submergence information derived from the SWS device of satellite transmitters (Hays *et al.* 1999). The present study was novel in the sense that dive profiles were obtained in combination with satellite locations, hence avoiding having to make assumptions about the positions of individual turtles from their depth utilisation and the bathymetry around the island (Hochscheid *et al.* 1999, Hays *et al.* 2000a, Houghton *et al.* 2002), or deriving diving behaviour from dive durations (i.e. long dive durations would reflect long dives on the sea bed, Hays *et al.* 1999).

Flat-bottomed dives to the sea bed have been described for other populations of Green turtles (e.g. Hochscheid *et al.* 1999) and for other species of shallow-diving sea turtles, such as Hawksbill turtles, *Eretmochelys coriacea* (van Dam & Diez 1996) and Loggerhead turtles (Houghton *et al.* 2002). The shape of a time/depth profile can sometimes give information about the activity in which the animal is engaged during the dive (e.g. diving mammals: Le Boeuf *et al.* 1988, diving birds: Chappel *et al.* 1993, Wilson *et al.* 1996). Particular dive types have often been linked to specific functions, such as hunting, searching for prey, travelling and food processing (e.g. Schreer *et al.* 2001). With regards to sea turtles, flat-bottomed dive profiles can equally result from benthic foraging or from resting behaviour (Hays *et al.* 2002c). For Hawksbill sea turtles, the depth during the bottom phase of foraging dives varied constantly, in contrast to the flat-bottomed resting dives they also performed (van Dam & Diez 1996). Also, activity sensors have been used on Green turtles in Cyprus to discriminate between different behaviours that could result in similar dive profiles (Hochscheid *et al.* 1999): this allowed the discrimination between benthic resting behaviour and benthic foraging behaviour (on beds of sea grasses), both resulting dive profiles being U-shaped. Hays *et al.* (2000a) hypothesised that the U dives performed by Green turtles during their inter-nesting period at Ascension Island reflected a combination of predator avoidance and resting (see Introduction of this chapter). However, it is now possible to add further evidence pointing towards U dives being resting dives.

Firstly, swim speed values may indicate whether there is swimming activity during the bottom portion of U dives. It was found that, for the one turtle that provided swim speed information (turtle 2), the swim speed during the bottom portions of U dives was virtually nil when compared to the swim speeds during the descent and ascent phases of U dives. Moreover, swim speed could be measured during the bottom portion of non-U dives, indicating that if there had been swimming activity during the bottom portion of U dives, then it could have been measured. These results clearly indicate that turtles do not swim during the bottom portions of U dives.

Secondly, dive durations are known to be closely inter-linked with activity levels in marine turtles (Hays *et al.* 2000b). Although the use of glide patterns during diving may not reduce speed by much and thus leads to energetic savings (Williams *et al.* 2000), swim speeds may be used, to an extent, as a proxy for activity levels (e.g. Elephant seal: Le Boeuf *et al.* 1992, Hindell *et al.* 2000; Bottlenose dolphin: Williams *et al.* 1993). In the present study, the fact that U dives tended to last longer than non-U dives, suggests that U dives present lower rates of oxygen utilisation than non-U dives. Consistent with this is the fact that the overall swim speed of non-U dives appeared faster than during U dives, which indicates that activity levels during non-U dives were likely to be greater than during U dives. Unfortunately, because dive duration entered in the calculation of the overall swim speeds for U and non-U dives (see Materials & Methods), it is impossible to statistically test for relationships between overall mean swim speed and dive duration, although one can expect that if there is a relationship, it is likely to be a negative one.

There was no consistent pattern of variation, across individuals, for the resting depths of U dives, neither with the hour of the day nor the day within the inter-nesting period. This may be the result of significant temporal gaps in the dive record for each turtle. By pooling the data for the four turtles, a diel pattern in resting activity was highlighted, with more resting dives taking place at night (consistent with Hays *et al.* 2000a), and more non-U dives occurring during the day than at night. The depth of the resting locations appears to be unrelated to the time of day or to the time within the inter-nesting period (except turtle 2), and might instead be more dependent on the relative suitability of different resting areas (e.g. location of predators, depth range; divers often observe turtles resting under rock ledges or at rock-sand interfaces; Mortimer & Portier 1989).

In the present study, maximum resting depths were hardly ever deeper than 19 m (N = 4 turtles), which was also the case for inter-nesting Green turtles in previous studies (Hays *et al.* 2000a: N = 6 turtles; Hochscheid *et al.* 1999: N = 2 turtles). Hays *et al.* (2000a) speculated that 19 m may represent the maximum depth at which Green turtles from Ascension Island can still attain near-neutral buoyancy after submerging with fully inflated lungs, and that beyond this depth, the increased lung compression leads to negative buoyancy (‘the 19 m hypothesis’). Resting passively on the sea bed at depths shallower than 19 m would be possible if turtles adjust their lung volume upon submerging (Minamikawa *et al.* 1997, 2000). In chapter 2 (p. 69-91), the consistent behavioural change around 19 m, as reflected by changes in the rates of vertical movement during the descent phases of type 2 dives, was attributed to turtles becoming negatively buoyant deeper than 19 m, thus providing additional support for the 19 m hypothesis.

The depth-duration relationship for U dives

In the present study, U dives tended to last longer when their maximum depths were deeper, a relationship previously reported by Hays *et al.* (2000a) for two turtles of Ascension Island. Similarly, dive durations increased with deeper residence depths (depths where turtles were neutrally buoyant) for Loggerhead turtles in Japan

(Minamikawa *et al.* 1997, 2000) and Green turtles in Cyprus (Hochscheid *et al.* 1999). Positive relationships between dive durations and depths have also been reported for other diving animals, such as phocid and otariid seals, and some diving birds such as penguins and Blue-Eyed shags (Le Boeuf *et al.* 1988, Croxall *et al.* 1991, Croll *et al.* 1992, Kooyman *et al.* 1992, Croxall *et al.* 1993, Boyd *et al.* 1995). These were, however, foraging dives, and the positive relationship between depth and duration was a consequence of the maximisation of foraging time whilst underwater.

In contrast, shallow diving sea turtles are thought to be neutrally buoyant during the bottom phases of these long duration dives, and consequently, the depth of residence is closely linked with the volume of air trapped in the lungs upon leaving the surface (Minamikawa *et al.* 1997, 2000). As a result, the deeper the depth of residence, the greater the lung volume (and hence the volume of oxygen stored) upon submerging, and the longer the resting dive can last (assuming a constant diving metabolic rates). It has appeared difficult, however, to accurately predict the duration of a resting dive to the sea bed from its maximum depth, i.e. the r^2 value obtained from regression analysis was 0.16 (this study) and were 0.27 and 0.69 in a previous study (Hays *et al.* 2000a). This suggests that using central tendency statistics (i.e. regression analysis) may not be optimal for investigating depth-duration relationships in resting Green turtles. Indeed, whilst the diving metabolic rate and the size of the oxygen stores at the start of the dive can be used to calculate the maximum aerobic time underwater (also called the 'aerobic dive limit', or ADL, Boyd 1997, Butler & Jones 1997, Costa *et al.* 2001), physiological limits may not be approached during resting, in contrast to during foraging dives.

The ADL is defined as the maximum duration of a breath-holding dive, without any increase in plasma lactate levels compared to resting, during or following a dive (Kooyman 1989), and it is generally used to model the diving metabolism by stressing the physiological constraints acting on the behaviour of diving animals (Castellini *et al.* 1992). During resting dives, physiological limits are comparatively less likely to be approached and, in addition, factors such as disturbance, motivation or light levels may influence when a dive will terminate. The fact that the turtles tend to return to the surface with partially depleted oxygen stores explains the large variance in the duration versus maximum depth plots, and thus is consistent with the resting function of U dives.

It is possible to define a line that will, at least, describe a boundary that limits the dive duration for each resting depth. Such a boundary may be called the 'ADL line', which represents a physiological constraint to dive duration and should contain all the resting dives. To build ADL lines for each turtle, it is necessary to estimate their diving metabolic rates and the size of their oxygen stores (lungs, blood and muscles) upon leaving the surface. The following method was adapted from Hays *et al.* (2000a).

Estimating the size of the oxygen stores:

The mass (in kg) of a turtle can be estimated from the Curved-Carapace-Length (CCL, in cm) by using the equation given in Hays *et al.* (2000a):

$$\text{mass} = 4.585 \times \text{CCL} - 349.22$$

From the mass can be estimated the lung capacity (as being 9.4% of mass, Berkson 1966) and the oxygen content of the blood and tissues (as being 6.7 ml O_2 kg^{-1}, Lutz & Bentley 1985). Since the maximum depths of U dives by Green turtles from Ascension are very rarely deeper than 19 m (Hays *et al.* 2000a, this chapter), 19 m is thought to be the depth at which neutral buoyancy is achieved if the turtle inhaled fully before diving. For each U dive to a given maximum depth, the corresponding lung volume upon leaving the surface can be estimated using the method already described in chapter 2 (p. 80) and the O_2 content of the air in the lungs is assumed to be 17.4% (Berkson 1966) at the start of the dive.

Estimating the diving metabolic rate:

The Resting Metabolic Rate (RMR, in l of O_2 kg^{-1} h^{-1}) was chosen as the diving metabolic rate, and was estimated using the regression equation provided in Prange & Jackson (1976):

$$\text{RMR} = 0.058 \times \text{mass}^{-0.174}$$

where mass is in kilograms (kg).

Estimating the ADL for each resting depth:

For example, the oxygen content of the blood and tissues for turtle 1 is $173.4 \times 0.0067 = 1.16$ l of O_2, and its RMR will be $0.058 \times 173.4^{-0.174} = 0.02365$ l of O_2 kg^{-1} h^{-1}. The lung capacity is $173.4 \times 0.094 = 16.29$ l of air and the lung volume at the depth of neutral buoyancy (19 m if the turtle dives with fully inflated lungs) is $(1 \times 16.29)/ 1.9 = 8.57$ l of air (1.9 ata is the hydrostatic pressure at 19 m). If turtle 1 performs a U dives to

15 m, the corresponding lung volume upon leaving the surface is (1.5 × 8.57)/ 1 = 12.86 l of air (1.5 ata is the hydrostatic pressure at 15 m), which contains 0.174 × 12.86 = 2.23 l of O_2. Hence, turtle 1 has a total oxygen store of 1.16 + 2.23 = 3.39 l of O2 at the start of a U dive to 15 m. The same calculation is run for each resting depth and each turtle. The relationship between total oxygen and resting depth reaches a plateau at 19 m because this resting depth corresponds to the lung capacity (figure 3-10, p. 125 shows this relationship for turtle 1).

The theoretical ADL for each resting depth is then calculated by dividing the estimated total on-board oxygen stores (blood, tissue, lungs) at the start of the dive by the estimated diving metabolic rate (Schreer *et al.* 2001), here the RMR:

ADL = oxygen stores / (RMR x mass)

For turtle 1 resting at 15 m, the ADL is 2.23 /(0.02365 × 173.4) = 0.54 hours, which corresponds to 32.6 minutes.

After calculating this ADL for each individual (some parameters of this calculation are shown in table 3-7, p. 125), it was found that turtles 1, 2 and 4 rarely exceeded their estimated ADLs during their U dives, confirming that physiological limits are not approached during resting. Indeed, less than 5% of their dives lasted longer than the estimated maximum dive duration for that resting depth (figure 3-11 A, B & D, p. 126). In contrast, about 30% of turtle 3's dives exceeded their estimated ADLs (figure 3-11 C, p. 126). Did turtle 3 make use of anaerobic metabolism during the dives that appear to be outside of the boundary line? Most air breathing marine animals generally dive well within their aerobic capabilities (marine mammals and birds: Kooyman *et al.* 1981, Hudson & Jones 1986, Castellini *et al.* 1992, Carbone & Houston 1996, Boyd 1997, Butler & Jones 1997, Walton *et al.* 1998, Bennett *et al.* 2001, Thompson & Fedak 2001; sea turtles: Lutz & Bentley 1985). This is because anaerobic metabolism incurs substantial energetic costs for diving, yielding only 1/18 of the total energy of aerobic metabolism, whilst the accumulation of lactate in the blood and tissues requires relatively long recovery times at the surface (Carbone & Houston 1996, Boyd 1997).

Because of the surfacing behaviour of turtles performing deep and long dives (i.e. post-dive intervals remain relatively short), it is widely believed that dives are aerobic for Green and Hawksbill turtles (van Dam & Diez 1996, Hochscheid *et al.*

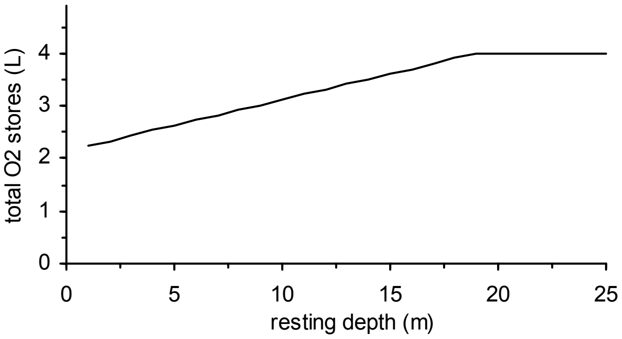


Figure 3-10. The relationship between total oxygen stores (lungs, blood and tissues) and the resting depth (turtle 1, see text and Hays *et al.* 2000a for details of this calculation).

Turtle	CCL (cm)	Estimated body mass (kg)	Estimated lung capacity (l)	ADL at – 19 m (min)
1	114	173.4	16.3	58.3
2	118	191.8	18.0	59.4
3	113	168.8	15.8	58.0
4	112	164.3	15.4	57.9

Table 3-7. Curved carapace lengths (CCLs), from which body mass and lung capacity were estimated, and the estimated aerobic dive limit for resting at 19 m (see text and Hays *et al.* 2000a for details of these calculations).

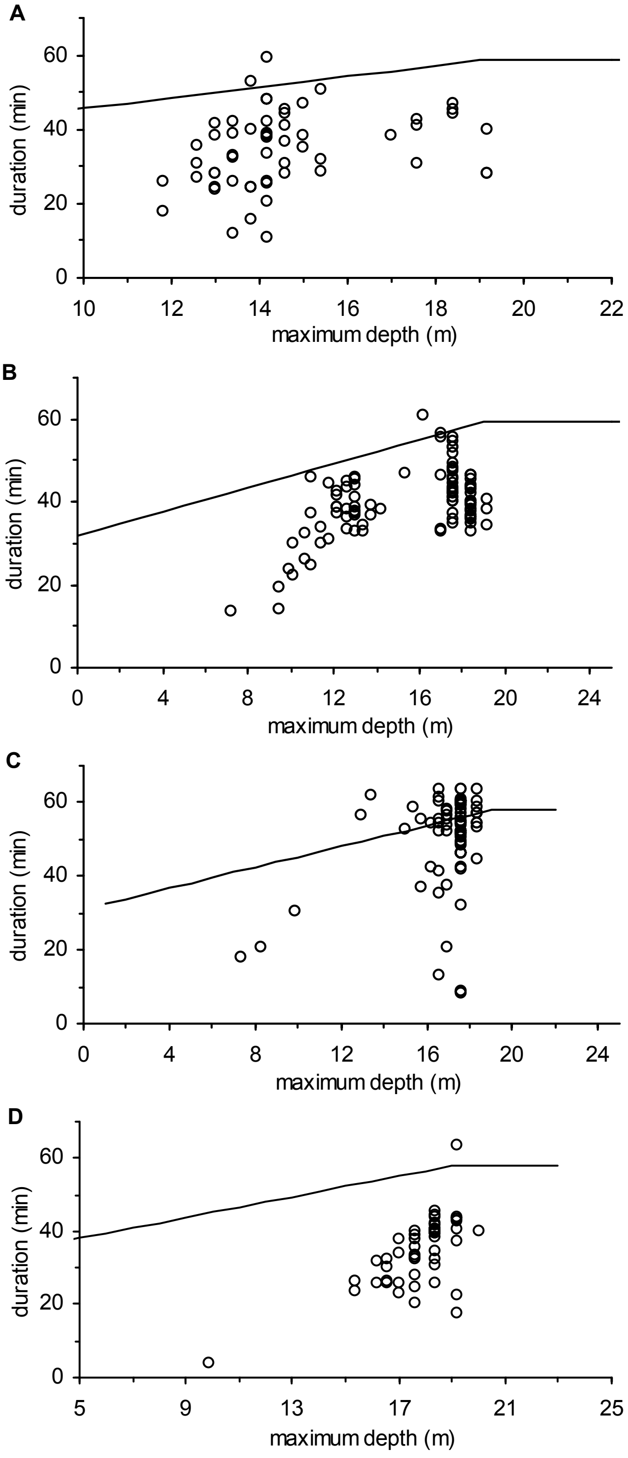


Figure 3-11. Same as figure 3-7 A-D, p. 112, except that the ADL lines are shown.

1999, Hays *et al.* 2000a). Laboratory experiments have shown that the Loggerhead turtle, another shallow-diving sea turtle, tends to perform voluntary dives that are fully aerobic (Lutz *et al.* 1989, Lutcavage & Lutz 1991).

A better way of explaining why turtle 3 appeared to have exceeded its aerobic capacity whilst performing U dives, is to return to the calculation of each ADL line. It is possible to perform a sensitivity analysis on some of the main aspects of this calculation: (1) the estimation of body mass from the curved-carapace-lengths, (2) the value of the diving metabolic rate and (3) the depth at which neutral buoyancy should be achieved when leaving the surface with fully inflated lungs:

(1) If the mass of turtle 3 varies by ± 50 kg, then the ADL at 19 m is found to vary by ± 2.7 minutes, thus an insignificant variation in aerobic capacity.

(2) For turtle 3, a resting metabolic rate of 0.02376 l of O_2 kg^{-1} h^{-1} is predicted to be sufficient to cover oxygen demands for 60 minutes (i.e. the ADL is 1 hour). If 0.02376 l of O_2 kg^{-1} were enough to cover oxygen demands for 65 to 70 minutes of resting, then the resting metabolic rate would become 0.02193 and 0.0203 l of O_2 kg^{-1} h^{-1} respectively, i.e. 7.7 to 14.6% lower than the resting metabolic rate that would allow it to stay aerobic for 60 minutes underwater. Hence, if the resting metabolic rate varies by about 15%, then the consequences on the aerobic time available at depth are substantial (more than 10 minutes). To illustrate this point, figure 3-12 (p. 128) shows how the ADL line is altered when the resting metabolic rate varies by ± 20%.

(3) If turtles, leaving the surface with fully inflated lungs, are assumed to reach neutral buoyancy at 14 m or 24 m (instead of the 19 m hypothesis), then the ADL at the maximum depth of neutral buoyancy (i.e. at 14 m or 24 m) remains unchanged. However, the ADL line reaches its plateau value quicker when the maximum depth of neutral buoyancy is 14 m than when the maximum depth of neutral buoyancy is 24 m. Hence, if the maximum depth of neutral buoyancy is altered in such ways, solely U dives to relatively shallow depths would see a change in their position with regards to the ADL line.

The estimation of the diving metabolic rate appears to be a critical point in the calculation of the ADL lines for resting turtles. The fact that estimates of diving metabolic rate drastically influencing the calculation of ADLs has been reported for other marine animals (e.g. Butler & Jones 1997, Costa *et al.* 1998, Nagy *et al.* 2001,

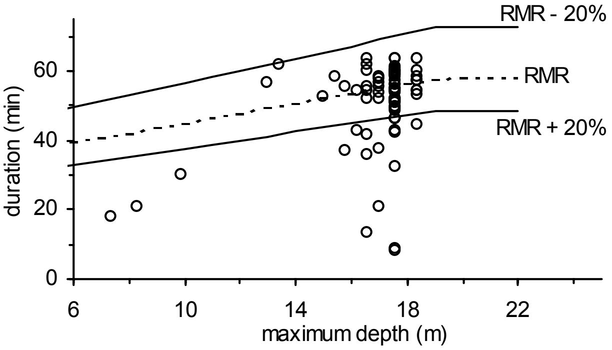


Figure 3-12. The relationship between duration and maximum depth during U dives (turtle 3), and the variation in the position of the ADL line when the value of the resting metabolic rate (RMR) is altered by ± 20% (see text for details).

Schreer *et al.* 2001). To estimate the diving metabolic rate of resting Green turtles, a regression equation was used based on measurements by respirometry on adult Green turtles resting on land (Prange & Jackson 1976). All Cheloniid marine turtles are ectothermic and it is possible that the resting metabolic rate of Green turtles in water, as compared to when on land, is in reality lower than that estimated using this regression equation. The relatively lower resting metabolic rates (about 30% lower) that Hays *et al.* (2000a) estimated from their model based on the depth-duration linear relationship of U dives by two Green turtles from Ascension Island are consistent with this.

The advantage of fitting a boundary line to the depth-duration relationship of U dives is that the line quantifies the effects of oxygen balance and diving metabolic rate, without attempting to account for all the variation in dive duration. The fact that turtles rarely reach their physiological limits during resting is clear in this type of analysis Therefore, although the predictions made using such boundary lines are limited to how long a dive could last, this type of approach characterises boundary conditions well, as opposed to central tendency statistics, such as regression analysis (Guo *et al.* 1998).

CHAPTER 4

How deep do Green turtle hatchlings swim?

INTRODUCTION

Movement on land, in water or in air, requires morphological, physiological and behavioural adaptations specific to the medium in which animals evolve. Since water is dense and viscous, hydrodynamic drag is a major force swimmers need to overcome when moving (Schmidt-Nielsen 1972, Alexander 1990), and is important in determining the energetic cost of transport for swimmers. With some simplifications, the total resistive forces encountered by swimmers consist of a complex combination of frictional, pressure and wave drags (Wu 1977); the last corresponds to the mechanical energy lost by making waves when moving at or directly underneath the surface. The magnitude of each type of drag depends on factors such as body size and shape, swim speed, the drag coefficient (which depends on the flow pattern around the body), and the physical properties of the fluid (Hind & Gurney 1997).

Although swimming near the air/water interface facilitates access to oxygen, swimming performance may be reduced as a result of the creation and propagation of surface waves, since they disperse energy (Webb *et al.* 1991). In his seminal work, Hertel (1966, 1969) investigated the influence of the depth of submersion on total drag, by towing spindle-shaped models in a water flume. He demonstrated that total drag became minimal when the dorso-ventral centre-line of the models was towed at a depth of at least 2.5-3 times their maximum thickness (also termed ‘body depth’). At this relative depth (and deeper), the wave drag component of total drag was minimised and the water surface remained undisturbed, i.e. no waves were generated at the surface. If, however, the models were towed increasingly nearer the surface, total drag progressively increased, until reaching a depth of about 0.5 times the maximum body thickness, where total drag became up to five times greater. Surface waves were also generated well before the models broke the water surface.

The marked difference of total drag, and consequently of transport cost, between ‘near surface’ and ‘deeply submerged’ movement has been illustrated for a wide range of species (e.g. Mallard duck, *Anas platyrhynchos*: Prange & Schmidt-Nielsen 1970; Rainbow trout, *Oncorhynchus mykiss*: Webb *et al.* 1991; see Videler & Nolet 1990 for a review). For instance, the total drag experienced by mink, seals and otters swimming at the surface has been shown to reach up to ten times the corresponding values when moving at the same speed whilst deeply submerged (e.g. North American mink, *Mustela* *vison*: Williams 1983; Harbour seal, *Phoca vitulina*: Williams & Kooyman 1985; Sea otter, *Enhydra lutris*: Williams 1989).

Given these studies, it seems surprising that comparatively little work has been carried out to determine exactly how deep free-ranging animals actually swim when they are travelling between locations. The reason for this lack of empirical data on routine swimming depths may be due to the fact that TDRs, which are now routinely used to measure the depth utilisation by various marine animals, have historically had rather poor depth resolution (often a precision of 2 to 5 m) meaning that near-surface dive depths cannot be resolved. Consequently, whilst it is very well known that many air-breathing marine vertebrates such as seals (e.g. phocid seals: Fedak & Thompson 1993), Sea lions (e.g. California Sea lion, *Zalophus californianus*: Feldkamp 1987), penguins (e.g. Adélie penguin: Chappell *et al.* 1993), sea turtles (e.g. Green turtle: Hochscheid *et al.* 1999), dolphins (e.g. Bottlenose dolphin: Skrovan *et al.* 1999) and whales (e.g. White whale, *Delphinapterus leucas*: Shaffer *et al.* 1997) generally avoid swimming at the surface for extended periods of time, their exact routine swimming depths are rarely reported. Hence, it is not yet known whether (1) these animals routinely swim at the shallowest depth to minimise total drag, and whether (2) this depth scales with their body size (i.e. larger animals tending to swim relatively deeper than smaller ones).

Sea turtle hatchlings provide a tractable group with which swimming depths can be examined. Under natural conditions, hatchlings crawl rapidly following emergence from their nest to the sea (Salmon & Wyneken 1987). Hatchlings normally enter the sea at night, and immediately begin a ‘swimming frenzy’ that may last up to 24 hours, during which they distance themselves from the shore and therefore from the shore-based predators (Carr 1952, Gyuris 1994). Since hatchlings swim both day and night during this frenzy and, since they swim slower than humans, direct observation of their swimming depths is possible. In essence, one would predict that two key factors might constrain the depth of swimming for turtle hatchlings during their frenzy period. By submerging, they avoid the high hydrodynamic cost incurred by surface swimming. Swim too deep, however, and the time and locomotor costs associated with this increased transit back and forth from the surface will rise. There should, therefore, exist an optimum depth for routine swimming. The aim of this study was to directly measure the swimming depths of Green turtle hatchlings during the early part of their swimming frenzy.

MATERIALS & METHODS

Fieldwork was conducted during May/June 2001 at Ascension Island. Nests from which hatchlings had just started to emerge were located during the day by the presence of tracks on the sand. Only the hatchlings found near the sand surface were selected for subsequent observation, as they would be the ones certain to emerge naturally on the next night. Hatchlings were kept in a quiet and humid atmosphere (in compartmented buckets), before and after the observations were made. During this period of time, the hatchlings were almost always quiescent, as they would have been in the sand. After observations of swimming depth were made (see below), hatchlings were returned to the bucket where they again became quiescent. During the next evening, i.e. when the hatchlings would have emerged naturally, hatchlings were released on the beach where they had been collected, and were allowed to crawl to the sea.

Straight carapace length and width, and maximum body thickness (i.e. body depth) were measured using a dial calliper (DialMax, Switzerland, 0.01 cm precision). The maximum body thickness is located at the level of the highest point of the carapace. Following the work of Webb *et al.* (1991), maximum body thickness was considered to be the vertical parameter for the scaling of swimming depth with body size.

Hatchlings generally emerge from their nest during night-time, as the darkness makes them less likely to be detected when crawling on the sand by visual predators. An important trigger for hatchling emergence is, however, sand temperature, and emergences may occur during daylight hours (Witherington 1991), for instance when rainfall has cooled the sand. Hence, although emerging at night may decrease the predation risk, daytime observations of swimming behaviour may still reflect natural behaviour.

Observations were carried out at high tide in the ‘turtle pond’ or in a sheltered bay (English Bay). The turtle pond is an enclosed pool (15 x 15 m, 1.30 m depth) that was formerly used to store adult Green turtles destined for the catering of passing ships.

The gate of the pond is presently broken, which allows very small waves to enter the pool at high tide. Since hatchlings are thought to predominantly orientate themselves at sea with respects to wave cues (Lohmann 1991), the turtle pond recreated almost natural conditions. The small waves in the pond were a sufficient stimulus for hatchlings to swim, but did not hamper accurate observations. The turtle pond was used when the water in English Bay was not sufficiently calm.

The human observer (the author) was trained to estimate depths underwater, whilst wearing a facemask and snorkel: she had to rapidly estimate series of random depths (range 0-20 cm) of a hatchling-sized model, held in the water by an assistant. When the observer became capable of estimating depth within 1-2 cm (figure 4-1, p. 135 is an illustration of this), she swam underwater behind one hatchling at a time, and at a constant distance of 1 to 2 m, ensuring she did not impede its natural swimming behaviour. When approached side-ways by the human observer, hatchlings clearly responded by changing their direction of movement in the direction opposite to the observer. In contrast, there was no obvious response by the hatchling when the observer followed it exactly from behind. Undisturbed behaviour was defined as straight-line, sub-surface swimming (Wyneken 1997). Powerstroke (synchronous movements of the front flippers) was used almost exclusively, except during surface intervals for breathing, where hatchlings used the dogpaddle motion (i.e. swimming with all four flippers, Salmon & Wyneken 1987). Such swimming has been recorded in the wild (Wyneken 1997), and are also reported for recently emerged Green turtle hatchlings, swimming in a water flume (Pilcher & Enderby 2001).

For each observed swimming dive (the first few dives after release are excluded), the maximum swimming depth corresponded to the bottom portion of the dive. It was estimated as the vertical distance between the longitudinal axis of the animal and the water surface. During the bottom portion of the swimming dives, depth was fairly constant and hence most of the dive time was spent at this depth, since descent and ascent portions represent small proportions of the dive time. The swimming behaviour of each hatchling was observed during short sessions (< 5 min), sometimes repeated after 15 minutes of rest (for the animal).

In order to test whether underwater swimming during the frenzy is part of a predator avoidance behaviour (rather than to solely avoid wave drag) some observations

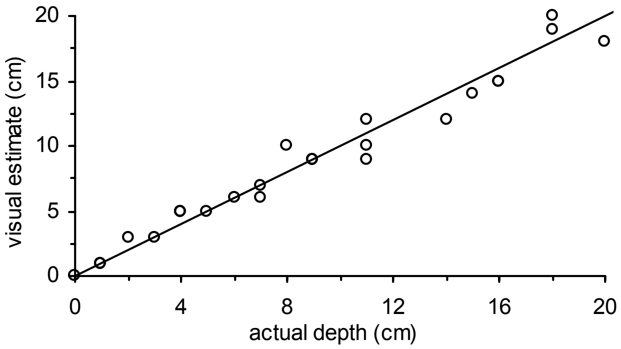


Figure 4-1. Accuracy of the human observer after training based on a random selection of 20 depths, ranging from 0 to 20 cm.

were made of the predatory behaviour of Frigatebirds (Fregatidae) on hatchlings, which had naturally emerged during the day.

RESULTS

The 47 hatchlings had a mean straight carapace length of 5.10 cm (SD = 0.13), a mean straight carapace width of 4.11 cm (SD = 0.23), and a mean maximum body thickness of 2.07 cm (SD = 0.06 cm) (figure 4-2 A-C, p. 137).

The maximum depths of swimming dives (at least five swimming dives per turtle) were noted, generating a total sample of 675 observed swimming dives. A total of 30 hatchlings were observed in the turtle pond. When an observed hatchling reached the other side of the pond, it was gently recaptured, re-observed or placed back into the bucket (awaiting for its evening release). For observations carried out in English Bay (*N* = 17 hatchlings), the observed hatchling was released in the water, a few metres from where the waves broke (and then re-captured after observation, for an evening release).

The mean maximum depths of the swimming dives recorded in the turtle pond (8.0 cm, SD = 4.1 cm) were close in absolute terms to those recorded in English Bay (6.1 cm, SD = 2.5), and were not significantly different (unpaired t-test, t = 1.95, p = 0.057, df = 44). Furthermore, much of the 1.9 cm difference in mean swimming depths between the turtle pond and English Bay was due to two hatchlings, performing relatively deep swimming dives in English Bay. Therefore, all the data collected in the turtle pond and in English Bay were pooled for analysis.

Maximum depths of individual swimming dives ranged from 2 to 51 cm (figure 4-3 A, p. 138), although dives deeper than 30 cm were extremely rare (*N* = 38 out of 675 swimming dives), and were probably caused by disturbance (these dives were still included in the analysis as it was unclear whether they were disturbed or not). The mean maximum swimming depths for each turtle ranged from 2.6 cm (*N* = 5 swimming dives, SD = 0.5 cm, SE = 0.2 cm) to 20.6 cm (*N* = 48 swimming dives, SD = 12.1 cm, SE = 1.7) (figure 4-3 B, p. 138). The overall mean maximum swimming depth (i.e. determined from the mean value for each of the 47 turtles) was 7.4 cm (*N* = 47 hatchlings, SD = 3.7 cm, SE = 0.5 cm, range: 2.6 – 20.6 cm). Even though the mean maximum swimming depths varied significantly between individuals (one-way Anova,

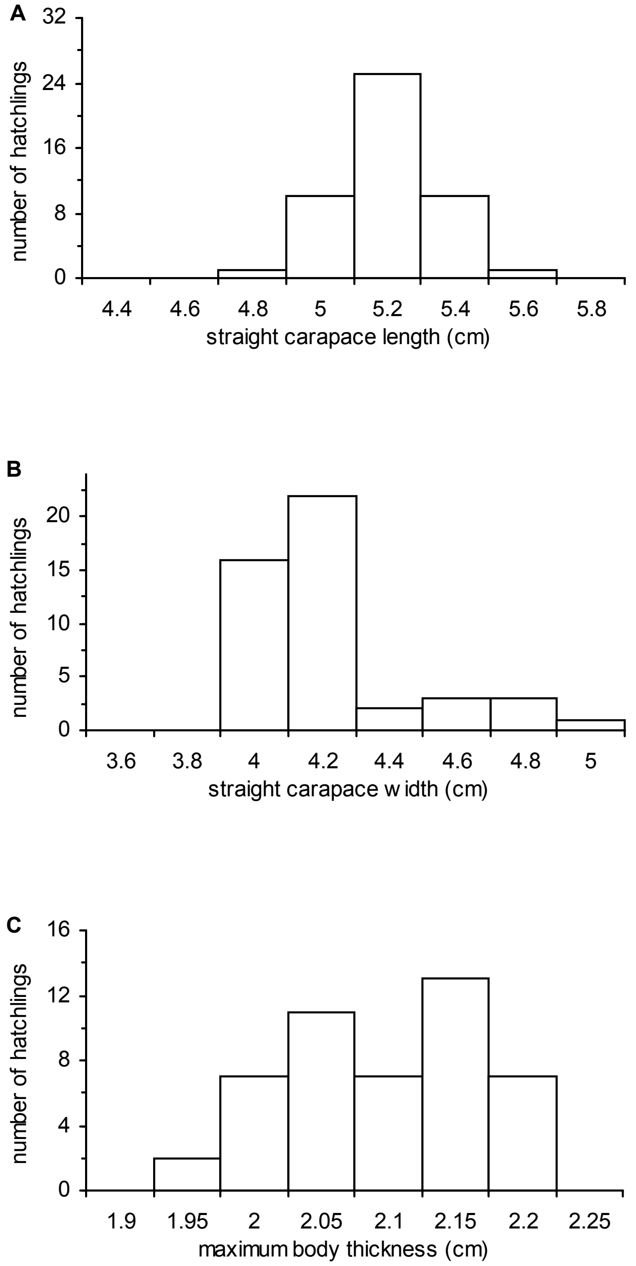


Figure 4-2. The frequency distributions of (A) straight carapace lengths, of (B) straight carapace widths and of (C) maximum body thickness ($N = 47$ hatchlings).

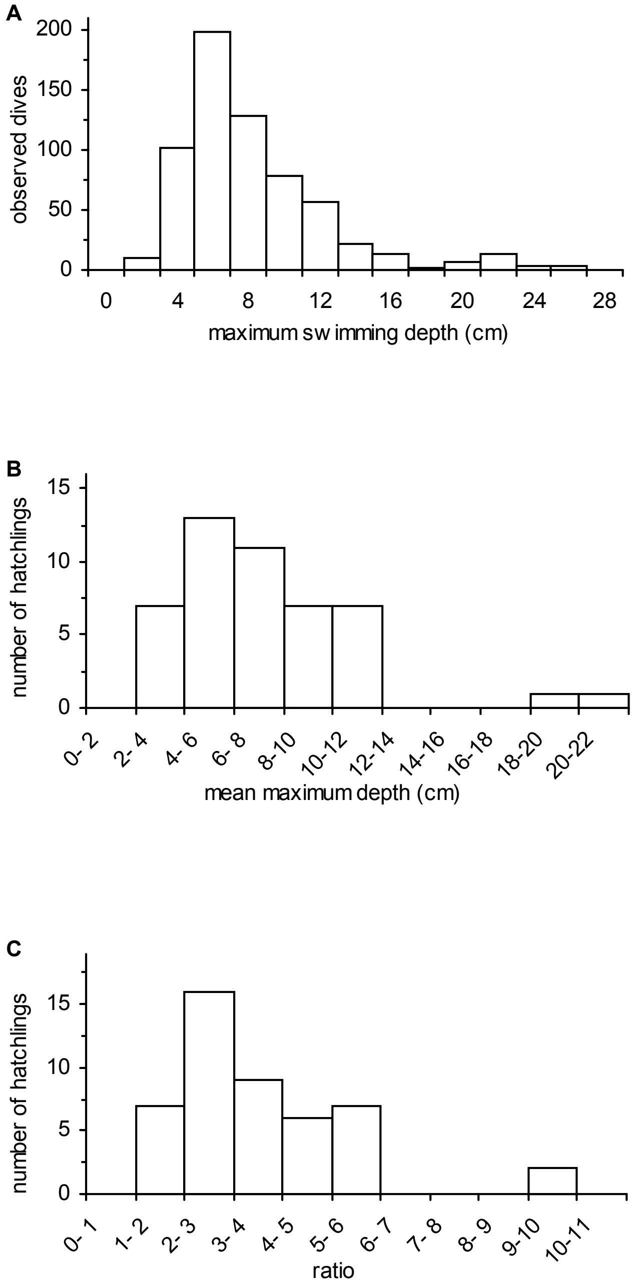


Figure 4-3. Frequency distributions of (A) the maximum depths of all the swimming dives observed (*N* = 675 swimming dives, 38 dives are out of scale), of (B) the mean maximum swimming depths (*N* = 47 hatchlings), and of (C) the ratios of the mean maximum swimming depths by the maximum body thickness (*N* = 47 hatchlings).

N = 47 hatchlings, $F_{0.05, 46, 520} = 6.82$, $p < 0.001$), none of the hatchlings were ever observed swimming at the water surface for extended periods of time. Finally, hatchlings swam at a mean relative distance of 3.5 (SD = 1.7, SE = 0.2, range: 1.2 – 9.7) times their maximum body thickness below the water surface. A high percentage (85%) of the 47 individuals swam, on average, at a relative depth of two to five times their maximum body thickness (figure 4-3 C, p. 138).

Frigatebirds were observed feeding on hatchlings that were crawling on sand towards the sea, after having emerged naturally during the day. Similar observations were made, near the shore, of Frigatebirds feeding on swimming hatchlings, which had managed to reach the water after having emerged during the day.

DISCUSSION

In order to study their frenzy and post-frenzy periods, their orientation capabilities, or their swimming and diving behaviours, turtle hatchlings have been tracked at sea, by boats or human swimmers (Frick 1976, Salmon & Wyneken 1987, Witherington 1991). Also, experimental studies using video cameras have been carried out in order to investigate, in detail, the swimming and diving behaviours of hatchling and juvenile sea turtles in the laboratory (Davenport & Clough 1986, Davenport & Pearson 1994, Davenport *et al.* 1997). Meanwhile, detailed investigations into the depths at which free-ranging Green turtle hatchlings swim remain scarce. Free ranging Cheloniid hatchlings are known to occasionally dive to depths of 3 to 4 m, but are mostly reported to swim 'within 1 m of the surface' (Wyneken 1997). Frick (1976) reported that tracked Green turtle hatchlings would swim underwater at an average depth of 20 cm or less, diving at varying intervals to about 3 m. Finally, Green turtle hatchlings, recently emerged from their nest, were found to swim 'approximately 5-10 cm' below the surface during trials in a re-circulating water flume (Pilcher & Enderby 2001). In this last study, it was shown that enforced captivity of turtle hatchlings in hatchery operations (similar to keeping hatchlings in a bucket, as in the present study) decreases swimming performance, but the main observed effect was a decrease in the hatchling's swimming speeds, whilst swimming depths were not mentioned to be affected by retention time.

Using very low cost observational techniques, new insights into the swimming depths of Green turtle hatchlings during the early frenzy period have been given. The present study aimed at answering two basic questions: ‘do Green turtle hatchlings swim submerged?’, and if so, ‘do their routine swimming depths scale with their body size in a way that would theoretically minimise total drag?’ Admittedly, the logical follow up to this study would involve using more ‘high-tech’ pieces of equipment such as underwater video cameras (for more accurate measurements of swimming depths) and a water flume (for measuring the progressive increase of total drag with shallower towing depths). Even though the hatchlings of the present study swam at variable depths, sustained swimming never occurred at the surface, or directly beneath it. Furthermore, the water surface directly above the bottom portion of the swimming dives remained undisturbed, indicating that hatchlings were swimming sufficiently deep to avoid creating surface waves.

In the present study, the observation of more than 600 swimming dives revealed that hatchlings swam, on average, slightly deeper than three times their maximum body thickness, and generally not much deeper than that. Although visual estimates of depth are bound to give approximate results, this large sample of dives increases the confidence in the results. This key behavioural adaptation is believed to allow hatchlings to minimise their cost of transport, most possibly *via* the minimisation of wave drag. In essence, it is generally thought that hatchlings attempt to maximise their offshore swimming distance during the swimming frenzy, so they get as far away as possible from high inshore predator abundance. Since hatchlings rely on stored energy reserves throughout their swimming frenzy, factors reducing their energetic cost of transport will, in turn, increase the distance covered. The life history of sea turtle hatchlings is such that a hatchling’s ability to navigate and swim rapidly away from its natal beach is a major requirement for survival (Wyneken & Salmon 1992, Gyuris 1994). Hence, optimising their swimming depth would be expected to have a strong selective advantage by optimising the use of limited energy reserves, therefore minimising the probability of mortality during offshore migration. When emerging naturally, such behavioural adaptation would enable hatchlings to reach offshore currents and evade near-shore predators, during valuable hours of darkness. The fact that turtle hatchlings do not routinely swim much deeper than about three times their body thickness below the surface may result from the combination of two factors: (1) the periodical need for oxygen with minimal transit costs and (2) the energetic cost of overcoming their buoyancy resistance (Davenport & Pearson 1994).

It might be argued that hatchlings swim submerged, not to avoid the high near-surface drag layer, but to be less visible from visual predators, such as Frigatebirds. In fact, observations of Frigatebirds catching hatchlings that are swimming offshore in the clear waters surrounding Ascension Island have been made, suggesting that the routine swimming depths do not provide a very efficient camouflage against such predators. Hence, predator avoidance cannot explain the routine swimming depths of hatchlings during the swimming frenzy, but rather, might explain the occasional deep dives seen both in this study and elsewhere (Frick 1976, Wyneken *et al.* 1994). Hatchlings may also swim submerged to keep their body at a given distance from the surface, in order to avoid their front flippers from breaking the surface (since this would generate more drag) during part of the flipper-beat cycle. Overall, the swimming of turtle hatchlings during the swimming frenzy may not be due exclusively to hydrodynamics, but rather a balance between hydrodynamics (believed to be the major factor) and other factors, such as positive buoyancy, high oxygen demand, behavioural cues used for orientation and anti-predator behaviour. This complex combination of factors could, in turn, partly explain the rather wide range of mean swimming depths (and their large standard deviations), which were recorded during this study.

The effects of wave drag would be expected to scale with body size, i.e. if animals do routinely swim at 2.5-3 times their body depth below the surface, then larger animals should swim deeper, in absolute terms, than smaller ones. This prediction is supported by the diving of migrating adult Green turtles: during their sub-surface travelling dives, turtles were shown to spend most of the dive time at 0.9-1.5 m, which corresponds to a relative depth of 2.5-4 times their maximum body thickness (Hays *et al.* 2001a). Although there is little empirical data on routine swimming depths for other species, Williams *et al.* (1992) nevertheless reported that free swimming dolphins preferred to swim at about 1 m below the water surface, i.e. at roughly 2.5 times their maximum body thickness. Finally, Webb *et al.* (1991) showed that the fast-start performance of Rainbow trout was significantly reduced when the fish were situated less than approximately 2-3 body depths (as measured by the caudal fin span) below the water surface, i.e. when fast-start occurred in the high-drag layer. Hence these studies on animals of different sizes suggest that depth selection, in order to minimise transport costs, might be a general behavioural adaptation that has evolved independently in separate taxa, as part of their suite of adaptations for living in an aquatic environment.

CHAPTER 5

The temporal occurrence of Leatherback turtles in the Bay of Biscay (1979-2000)

INTRODUCTION

The Leatherback turtle has a wide geographical distribution and, although nesting generally occurs on exposed tropical beaches (approximately between 40°N and 35°S), its foraging grounds appear widespread across ocean basins. A long-distance migrant, its presence has been well-documented in temperate waters, notably in the north American and European Atlantic waters, where it is a regular visitor and considered a regular and normal member of the marine fauna (Carr 1952, Brongersma 1972, Brongersma 1995). This rather fascinating animal has stimulated public and scientific interest over centuries, although in the Middle Ages, a large Leatherback turtle would probably have been classified as a 'sea monster' (e.g. Brongersma 1972). In more recent times, this large marine reptile has proved to be readily identifiable because of its unique soft-shelled appearance and great size, which may explain why its sightings are relatively more frequently recorded than those of other species of hard-shelled sea turtles in the same areas. Notably, the largest ever recorded individual was found stranded in the UK, weighed 916 kg and was over 2 m long (Eckert & Luginbuhl 1988).

There are distinct seasonal peaks in the occurrence of live Leatherback turtles in temperate waters. In New-Zealand, Leatherback turtle incidences tend to peak in the summer and autumn months (January-May, Gill 1997). On the North-Eastern US and Canadian coasts and in Monterey Bay (California), the sightings of live individuals tend to peak late in the summer (August/September, Prescott 1988, Shoop & Kenney 1992, Starbird *et al.* 1993, Kenney 1996). In contrast, seasonal peak incidences tend to be shifted earlier in time the further south on the Eastern US coast (March/May, Epperly *et al.* 1995, Grant *et al.* 1996, Dodd & Mackinnon 2000). In European Atlantic waters, most turtles are reported between August and October, with peak incidences being reported around August (Brongersma 1972, Godley *et al.* 1998, Pierpoint 2000). Dead turtles are usually reported for a greater proportion of the year and tend to peak slightly later than the sightings of live individuals (Prescott 1888, Pierpoint 2000). In all cases, Leatherback turtles are generally infrequent, or absent, for the rest of the year (i.e. winter and spring months).

Information regarding the spatial and temporal occurrences of Leatherback turtles in the coastal waters of France is abundant in the French scientific literature (e.g. Mediterranean waters: Olivier 1986; Atlantic waters: Fretey & Girondot 1996). Of extreme interest are the long-term records (1979-2000) of incidental observations of live and dead turtles in the Bay of Biscay, on the French Atlantic coast. The Bay of Biscay, and especially one area called the ‘Pertuis Charentais’, has historically received more attention than other areas of the French coastal waters. This is probably because of the regular, seasonal occurrence of Leatherback turtles in these waters, at the end of each summer. This study presents the compilation of an extended dataset of incidental observations of live and dead turtles, made in the Bay of Biscay over twenty-two years (1979-2000). This is thought to be the first time that this information, which is obtained from annual publications, has been analysed over such an extended period. The present study has two broad aims: (1) to interpret the patterns of Leatherback turtle occurrence in the Bay of Biscay (1979-2000) and (2) to highlight any changes in the timing of the seasonal occurrence of turtles in this area.

MATERIALS & METHODS

Data collection

Twenty-two years of records (1979-2000) of Leatherback turtles were extracted from Duguy (1986a, 1986b, 1988a, 1988b, 1989, 1990, 1992, 1993, 1994, 1995), Duguy *et al.* (1980, 1997, 1998b, 1999, 2000b, 2001) and Duguy & Duron (1981, 1982, 1983, 1984, 1985, 1996). These records, which meticulously detailed each observation of a live or dead turtle, originated from sea patrols of the French national police, recreational vessels, local fishermen, local councils, members of the general public and volunteers of the sea mammal stranding network (CNEMM, since 1972). Data collection was historically centralised at the Natural History Museum of La Rochelle (46.1°N, 1.1°W, figure 5-1, p. 146), and subsequently at the Aquarium of La Rochelle. La Rochelle was also the geographical base of ship-board survey efforts. Surveys at sea were carried out most years, in calm weather, usually within about 10 miles off the French coast, and generally from June until September. Probably as a consequence of this geographical restriction, most of the records that resulted from the ship-board surveys being organised from La Rochelle (about 90% of the observations made at sea) were quite closely centred around 46°N-1.5°W, in an area called the ‘Pertuis Charentais’.

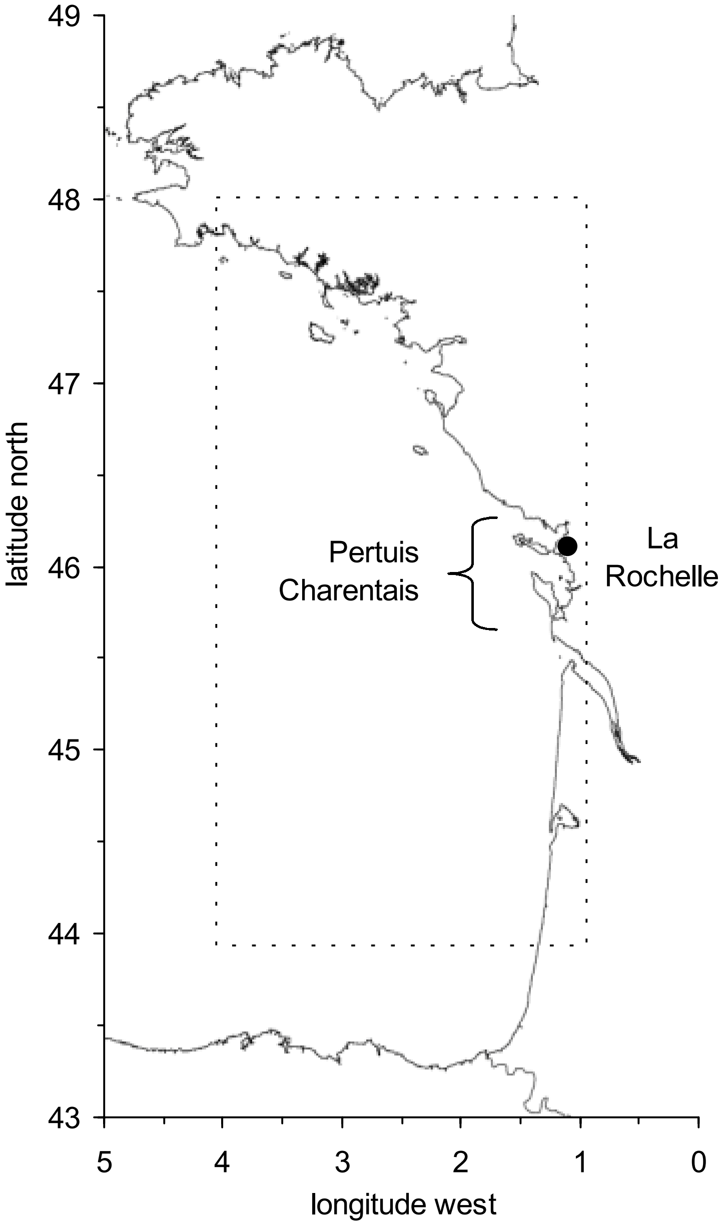


Figure 5-1. The Atlantic coast of France showing the Bay of Biscay and the study area (rectangle). The ship-board surveys organised from La Rochelle were mostly carried out in the Pertuis Charentais.

The record of a turtle observed at sea was defined as a ‘sighting’ (which could be a live sighting or a dead sighting), while the record of a turtle observed ashore was termed ‘stranding’ (which could be a live or a dead stranding). Capture events, usually involving fishing gear, were classed separately as live and dead ‘captures’. The locations of each record were usually (but not in all cases) provided in the publications. The exact date of each observation was nearly always provided, one significant exception being 1996 for which it was not possible to determine exact dates for 14 observations.

In order to examine temporal incidences, the day/month information of a record was computed as ‘day of the year’ (days 1-365). Since the seasonal distributions of ‘strandings’ generally overlapped two successive calendar years, stranding data were arbitrarily corrected to start at day ‘140’ (i.e. 20/05), whilst the days after the 31st of December then became ‘day 366’ (01/01), ‘day 367’ (02/01) and so on. The mean day of a seasonal distribution referred to the arithmetic mean of all the ‘days of the year’ obtained from records during a given period of time.

On several occasions, the date of an event was provided indirectly in an annual publication (e.g. *via* a histogram), this being the case mainly for some of the live sightings in years 1996, 1997, 1999 and 2000. Such data was corrected by allocating a ‘day of the month’ to any such incomplete record: for example an event occurring during 1-15 of a month would be classed as ‘day 8’ of that month (and similarly, a day during 15-31 would become day 23). It was believed that these corrections were unlikely to create any systematic temporal bias, although they may have accentuated noise.

The first part of the study was concerned with records (live sightings and dead strandings) originating from a sub-area of the Bay of Biscay, delimited by 44-48°N (≈ 445 km) and 1-4°W (≈ 241 km). This area was referred to as the ‘study area’ (figure 5-1, p. 146). The great density of information originating from this area during the study period allowed the investigation of temporal patterns of live sightings, whilst minimising spatial bias. Since Brongersma (1972) also reported some live sightings in this area of the Bay of Biscay (particularly for the period 1919-1969), the study also included some of this information (when the date of records was sufficiently precise). In contrast, information regarding dead strandings were only briefly looked at for reasons explained later.

In the second part of the study, records originating from other parts of the Atlantic European waters were examined (i.e. records from outside the study area). The aim was to put into perspective the general seasonal pattern recorded in the study area, by comparing it with patterns recorded in areas located north and south of it. For this purpose, information (live sightings only) was gathered (1) for the UK & Irish waters (Pierpoint 2000) and Norway (Brongersma 1972), (2) for the northern coast of France (Brongersma 1972 & publications by Duguy and co-workers, see above), and (3) for Spain and Portugal (Brongersma 1972). The data obtained from Brongersma (1972) was rather restricted in numbers because there was a relatively small number of records and only a few had adequate date information.

Sea Surface Temperatures

Sea Surface Temperature (SST) data were obtained from the Comprehensive Ocean-Atmosphere Data Set (or COADS, source: http://www.cdc.noaa.gov/coads). Monthly summary statistics for boxes of 1° of latitude and longitude were weighted to account for the number of observations in each box and averaged for each month of each year (1979-1997), for an area of the Bay of Biscay delimited by 45-47°N and 1-3°W.

RESULTS

Incidences of sightings and strandings for the French Atlantic coast

From the publications of Duguy and co-workers, a total of 1249 records for the Atlantic coast of France were gathered, with 1126 records originating from the study area, and 123 records originating from areas north and south of the study area (table 5-1, p. 149). For all areas, captures in fishing gear were relatively sporadic (N = 57, 1979-2000), and have been examined by Duguy *et al.* (1998a). For the period 1979-2000, dead sightings and live strandings were relatively infrequent (N = 27 and 4 respectively), compared to live sightings and dead strandings (N = 878 and 283

	Live/Dead	Study area	Rest of French Atlantic coast	Totals
Sightings	live	**804**	74	878
	dead	22	5	27
Strandings	live	4	0	4
	dead	**255**	28	283
Captures	live	28	11	39
	dead	10	4	14
	unknown	3	1	4
Totals	-	1126	123	1249

Table 5-1. Incidences of sightings, strandings and captures for the French Atlantic coast (1979-2000). The live sightings and dead strandings originating from the study area are highlighted in bold.

respectively). Because of the prevalence of observations originating from the study area, the analysis focused on those records.

Incidences of live sightings & dead strandings in the study area

For the study area, a total of 804 records of live sightings and 259 records of dead strandings (total = 1063) were compiled. Annual incidences for the study area, as directly based on these records, were relatively low from 1979 until the mid 1990s, but greatly increased thereafter (figure 5-2 A, p. 151). There was a sharp increase in the annual incidences of live sightings from 1996 to 2000 (with a maximum of 177 records in 1997), compared to annual incidences between 1979 and 1995 (with a maximum of 55 records in 1979). With regards to dead strandings, annual incidences were relatively low between 1979 and 1994 (with a maximum of 10 records in 1993), whilst annual incidences showed a remarkable increase from 1995 to 2000 (with a maximum of 55 records in 1995).

The incidences of live sightings were positively correlated with the incidences of dead strandings, for each year throughout the study period (linear correlation, $F_{0.05,\ 1,\ 21} = 6.9$, $r = 0.50$, $p = 0.015$). The year 1995 showed, however, a seemingly abnormally elevated number of dead strandings ($N = 55$ dead strandings; $N = 33$ solely for October). When this outlier was disregarded, the annual incidences of live sightings and dead strandings were extremely positively correlated (figure 5-2 B, p. 151; linear correlation analysis without year 1995, $F_{0.05,\ 1,\ 20} = 37.5$, $r = 0.81$, $p < 0.0001$).

Cumulated monthly totals (1979-2000, figure 5-2 C, p. 151) showed a clear and strong seasonal pattern, with more than 90% of live sightings occurring between August and September (range: May until November). In contrast, records of dead strandings spread over most of the year, with 88% of dead turtles being found between August and January (range: June until April the following year). There was also a clear time lag of two months between the peak of live sightings and that for of dead strandings. Finally, for each year between 1979-2000, the first live sighting always occurred earlier in the year than the first dead stranding.

Patterns of occurrence of live sightings and dead strandings in the study area

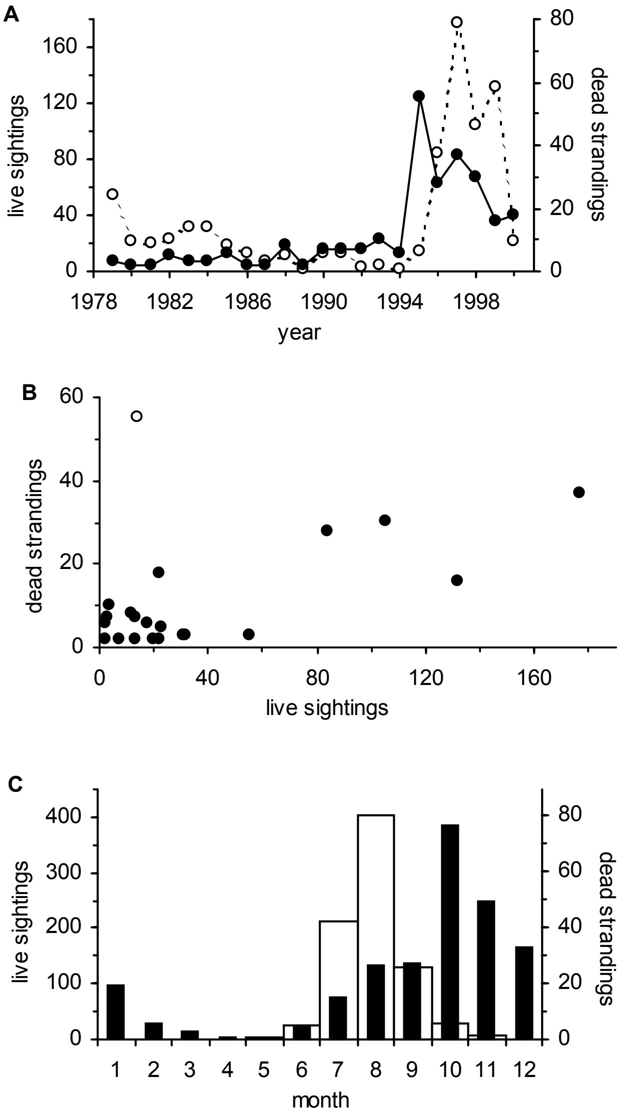


Figure 5-2. The incidences of Leatherback turtles in the study area (1979-2000). (A) The annual incidences of live sightings (o and primary y-axis) and dead strandings (• and secondary y-axis). (B) The relationship between the annual incidence of live sightings and that of dead strandings for the same year (•; 1995 is shown as o). (C) The patterns of occurrence (cumulated monthly records, 1979-2000) for live sightings (open bars and primary y-axis) and dead strandings (solid bars and secondary y-axis).

For a given record of a dead stranding, it was unknown for how long the dead/sick turtle had been drifting in the water before becoming stranded. Therefore, the data from dead strandings provided little information about the time of year when these turtles were alive in the study area. It consequently made little sense to calculate any descriptive statistics for any of the seasonal patterns of dead strandings (not to mention the problem of small sample sizes in some years).

Each live sighting provided, however, important information about the seasonal occurrence of Leatherback turtles in a given area. Furthermore, if some years presented small sample sizes (i.e. < 30 live sightings), it was possible to combine the data from successive years, to reach acceptable sample sizes (i.e. > 30 live sightings), with data typical for a given temporal window. The data were arranged into eight groups (groups B-I in table 5-2, p. 153) of live sightings (for data from Duguy and co-workers) by combining the data from one (or more) years, to obtain sample sizes of 30 live sightings or more. Year 1996 was disregarded since the exact date for 14 records could not be determined. One additional group (A) summarised the data obtained from Brongersma (1972) ($N = 20$ live sightings for 1919-1969).

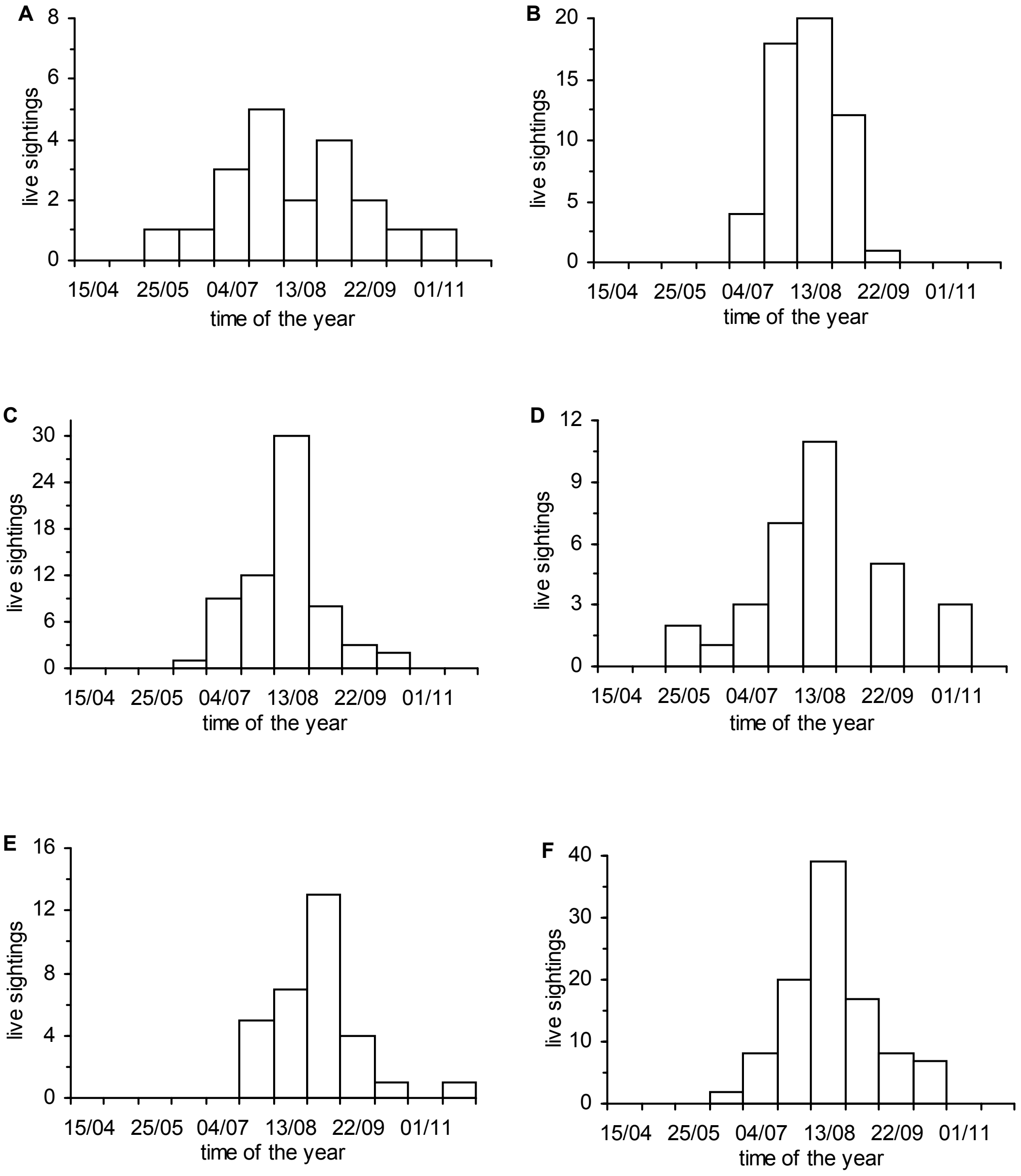
For the period 1979-2000, each of the eight groups showed a clear seasonal pattern of occurrence, with sightings peaking in August (figure 5-3 B-I, p. 154-155 and table 5-2, p. 153). In most periods, the seasonality was very similar, with mean days of the seasons ranging from 6th to 16th August. In addition, the mean day estimated for the period 1919-1969 (figure 5-3 A, p. 154, data from Brongersma 1972) was comparable to the values for 1979-2000 (although the 95% confidence interval for 1919-1969 was 18.5 days, table 5-2, p. 153). It was noticeable, however, that in 1984, live sightings tended to occur relatively later than the sightings of the other groups, with the mean day of the season being 28th August.

Sea Surface Temperatures in the study area

Monthly SSTs ranged from a minimum monthly value of 8.3°C (January 1981) to a maximum of 21.2°C (August 1997) and showed a strong annual periodicity (figure 5-4 A, p. 156). Long-term monthly SSTs (mean for each month, 1979-1997) revealed that the SSTs in the study area were warmest around August (curve in figure 5-4 B, p. 156), which was incidentally also the month when most live Leatherback turtles were

Groups	Fig. 5-3	*N*	Mean day	Calendar date	SD (days)	CI (days)
1919-1969[1]	A	20	222.2	10/08	±39.5	±18.5
1979[2]	B	55	221.4	09/08	±20.3	±5.3
1980-1982[2]	C	65	220.2	08/08	±24.6	±5.9
1983[2]	D	32	222.0	10/08	±38.9	±18.4
1984[2]	E	31	240.9	29/08	±24.4	±8.6
1985-1995[2]	F	101	227.7	16/08	±27.0	±5.2
1997[2]	G	177	224.1	12/08	±23.6	±3.4
1998[2]	H	105	226.7	15/08	±18.0	±3.4
1999-2000[2]	I	154	218.0	06/08	±25.4	±4.0

Table 5-2. Descriptive statistics for the nine histograms presented in figure 5-3 A-I (p. 154). *N*: number of live sightings during the period; Mean day: mean day of the year for each group, and its corresponding calendar date; SD: standard deviation of the mean; CI: confidence interval at 95%. [1]: data from Brongersma (1972), [2]: data from Duguy and co-workers (see Materials & Methods).


A
8
6
4
2
0
live sightings
15/04 25/05 04/07 13/08 22/09 01/11
time of the year
B
20
15
10
5
0
live sightings
15/04 25/05 04/07 13/08 22/09 01/11
time of the year
C
30
24
18
12
6
0
live sightings
15/04 25/05 04/07 13/08 22/09 01/11
time of the year
D
12
9
6
3
0
live sightings
15/04 25/05 04/07 13/08 22/09 01/11
time of the year
E
16
12
8
4
0
live sightings
15/04 25/05 04/07 13/08 22/09 01/11
time of the year
F
40
30
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10
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live sightings
15/04 25/05 04/07 13/08 22/09 01/11
time of the year

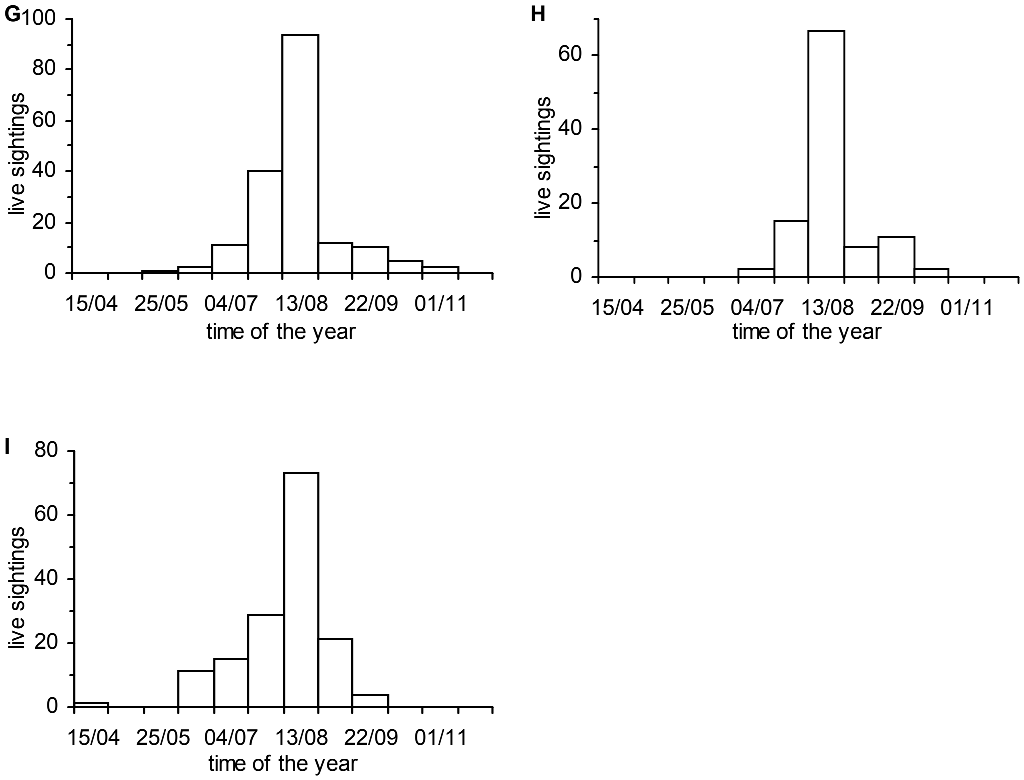


Figure 5-3. The patterns of occurrence of the nine groups of live sightings the study area (see table 5-2, p. 153, and text for details). (A) Data from Brongersma (1919-1969); (B-I) Data from Duguy and co-workers: (B) 1979, (C) 1980-1982, (D) 1983, (E) 1984, (F) 1985-1995, (G) 1997, (H) 1998, (I) 1999-2000.

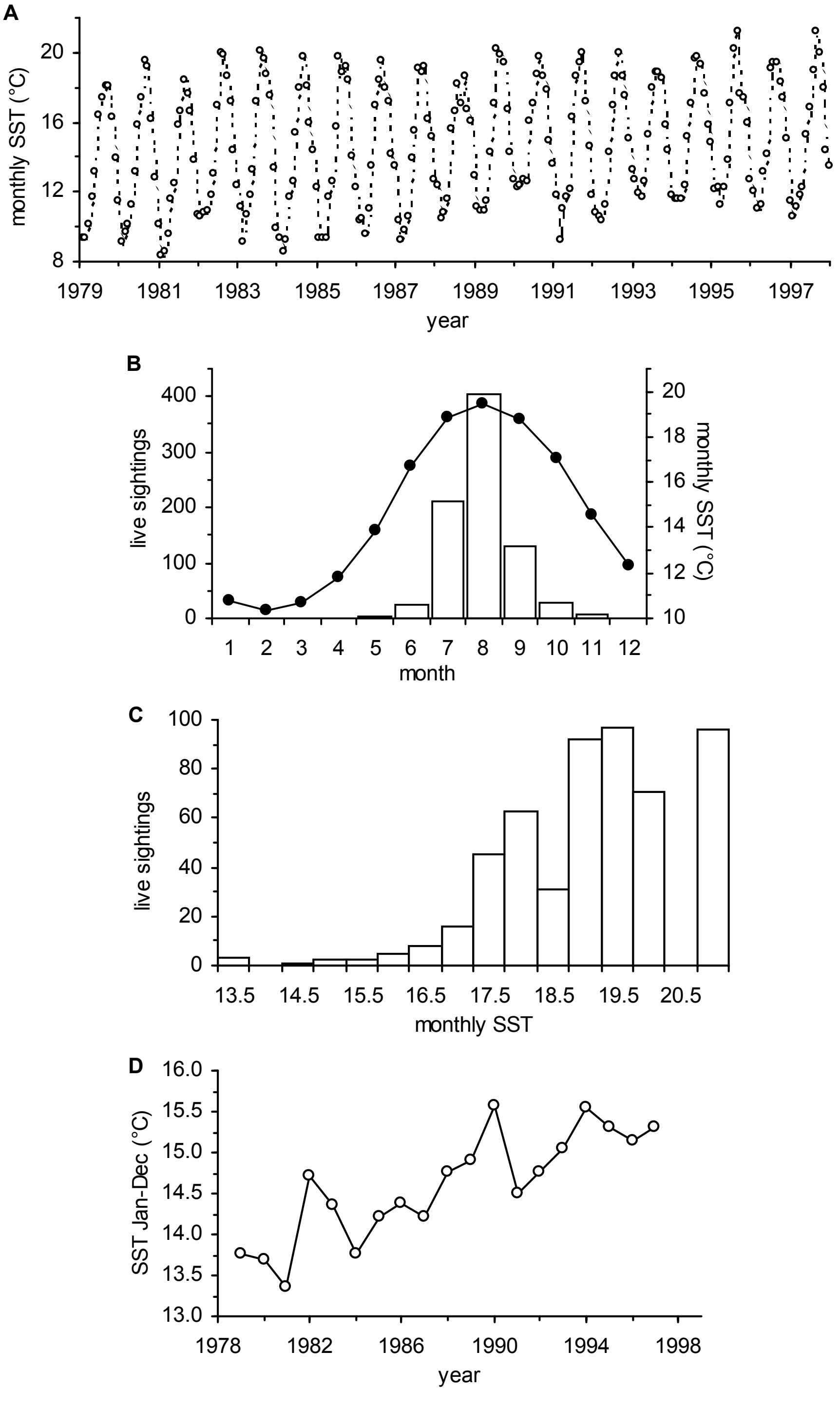


Figure 5-4. (A) The mean monthly SSTs for the study area (1979-1997). (B) The pattern of occurrence of live sightings (1979-2000, open bars, primary y-axis) and the monthly SSTs (mean for each month over 1979-1997; •; secondary y-axis). (C) For 1979-1997, the frequency distribution of live sightings that were associated with the monthly SST of their month of occurrence (*N* = 532 live sightings). (D) The SSTs (means for January-December) for the study area (1979-1997).

observed (open bars in figure 5-4 B, p. 156). In fact, sighting compilation for the period 1979-1997 showed that more than 85% of live sightings were made when monthly SSTs were between 18 and 21°C (figure 5-4 C, p. 156).

One might predict that variations in SSTs affect the timing of the occurrence of live sightings. For instance, live sightings might peak later if that year is on average colder, since this might delay the onset of warm summer SSTs. The mean annual SST in 1984 was indeed relatively cold (figure 5-4 D, p. 156), which could explain the relatively later appearance of live turtles in this year (table 5-2, p. 153, group E). Other years with comparatively cold SSTs (e.g. 1979, 1980, 1981, in figure 5-4 D, p. 156) however exhibited no variation in the timing of occurrences (table 5-2, p. 153, groups B & C), suggesting that there must be additional reasons for the late occurrence of live turtles in 1984.

Temporal patterns of occurrence of live sightings in and outside of the study area

Cumulated monthly records of live sightings showed a clear and strong seasonal pattern for the northern part of European waters (UK & Irish waters and Norway, figure 5-5 A, p. 158), a pattern very similar to that recorded in the study area (figure 5-5 C, p. 158). For both areas, peak occurrences were in August. The patterns recorded for the northern part of the French coastal waters (figure 5-5 B, p. 158) and for Spain and Portugal (figure 5-5 D, p. 158) were much less clear. This was probably a result of the small sample sizes used to describe these areas, which was due to the lack of precise dates for a majority of the 74 sightings provided by Duguy and co-workers.

DISCUSSION

Brongersma (1972) gathered a total of 188 records of Leatherback turtles for the whole of the European waters (ranging from Iceland to Portugal, mostly for 1900-1970), with about 84 records originating from the French Atlantic coast (although many had incomplete information). The extended dataset (more than one thousand records) for the French Atlantic coast (1979-2000) and, in particular for the Bay of Biscay, confirms the importance of European waters as a seasonal habitat for this species.

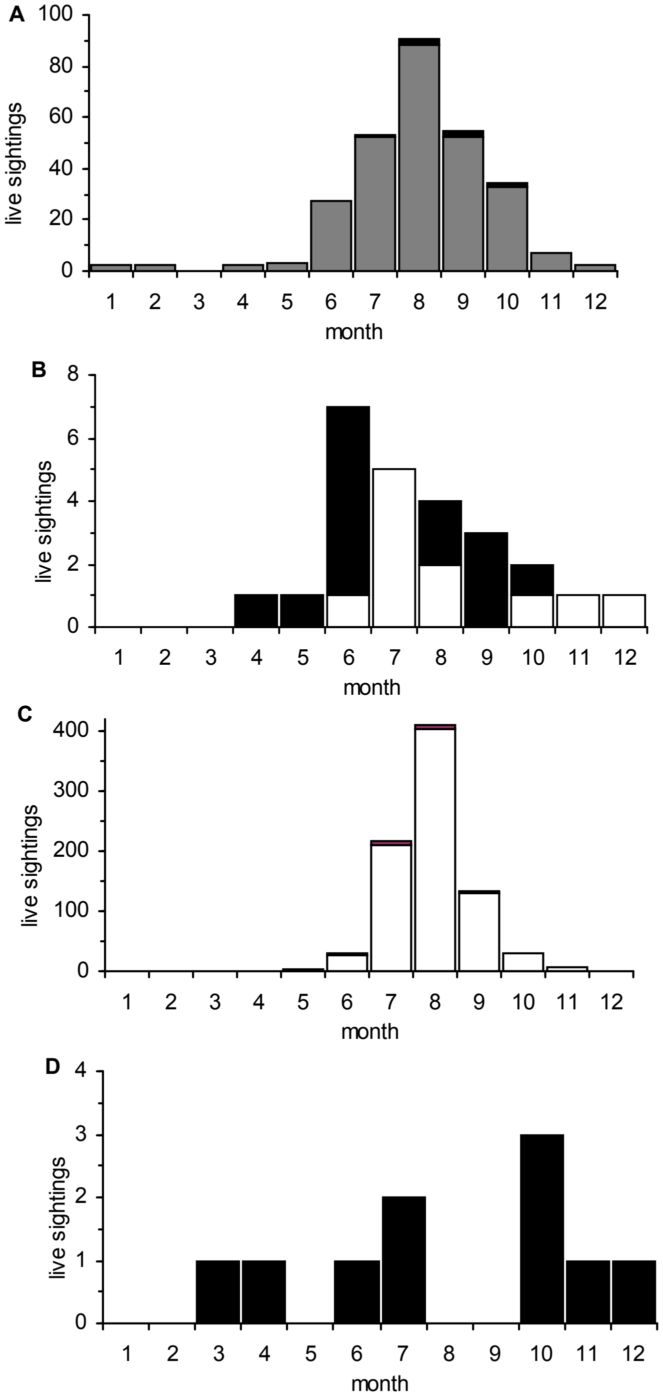


Figure 5-5. The patterns of occurrence (cumulated monthly records) for live sightings (see text for details). Dark bars: mostly 1900-1970 (Brongersma 1972), grey bars: 1950-1999 (Pierpoint 2000), open bars: 1979-2000 (Duguy and co-workers). (A) UK & Irish waters (*N* = 270, grey bars) and Norway (*N* = 8, dark bars), (B) Northern coast of France (*N* = 14, dark bars; *N* = 11, open bars), (C) study area (Bay of Biscay; *N* = 25, dark bars; *N* = 804, open bars), (D) Spain and Portugal (*N* = 10, dark bars).

Migratory movements into warmer waters from May-November appear typical of this turtle's normal ecology.

Incidences of live sightings and dead strandings in the study area

In the study area, annual incidences of live sightings and dead strandings showed some variability throughout 1979-2000, with dramatic increases in annual incidences from the mid-nineties. Similarly, the reporting rates for live Leatherback turtles between 1980 and 1999 varied greatly, on an annual basis, for the UK and Irish waters (although annual incidences always remained < 25 live sightings), with a continuous increase of reporting rates for each year between 1995-1999 (Pierpoint 2000). Brongersma (1972) also noticed significant variability in annual incidences and a gradual increase in the number of records since the beginning of the 20th century (1900-1970), as well as a 'sudden' and 'tremendous' increase in the number of records for 1950-1970. Inter-annual variability may be explained by annual variations in the absolute abundance of turtles visiting the area, and by other factors profoundly affecting recording efforts such as war (Brongersma 1972). More interesting are the various factors that may have contributed to the increase in incidences throughout the 20th century. Brongersma mentions a few factors, such as a growing interest in natural history, easier means of communicating the records to zoologists and museums, growth of human populations in western Europe, with people having longer vacations (more people coming to the shores will increase the probability of reporting strandings), and finally more intensive and extensive fisheries (more fishing vessels at sea with greater speed and greater manoeuvrability). These factors alone, however, may not be responsible for this increase and other factors, such as physical changes, may come into play. For instance, a slight rise in SSTs may make it possible for turtles to reach more northern waters, perhaps explaining the increase in incidences for the most northern parts of Europe (Brongersma 1972).

With regards to the more recent reports, information on the effectiveness of the reporting network over the years is scarce, and as is information regarding the intensity of the ship-board surveys. The comparatively greater incidences for both live and dead turtles from the mid-nineties appears likely to have resulted at least partially from a better awareness and utilisation of the existing reporting network (especially in the case of carcasses on land, since the physical evidence is longer-lasting than a short-lived sighting event at sea). However, for both the Bay of Biscay and UK & Irish waters, it is difficult to attribute the increase of annual incidences in recent years to improved reporting networks or greater observer effort alone. It is likely that there has been an increase in the absolute abundance of turtles visiting both geographical areas, although the influence of biological factors (e.g. prey density) and physical factors (e.g. SSTs) on their abundance is not yet well understood.

Patterns of occurrence of live sightings and dead strandings in the study area

Uneven levels of survey effort would cause important inconsistencies if the aim was to estimate population abundances. Although it is true that the ship-board surveys took place solely during the summer months, this bias is unlikely to be critical when investigating temporal patterns of occurrence, since it is well known that live turtles are extremely infrequent at other times of the year. The extended dataset (1979-2000) presented in this study confirms the strong seasonal patterns of Leatherback turtle occurrence in the Bay of Biscay, patterns that were originally identified by Duguy (1997). As in the UK & Irish waters (Godley *et al.* 1998, Pierpoint 2000), live sightings peak in August, with dead strandings tending to peak one or two months later.

Brongersma (1972) found that sightings of live turtles culminated in the first half of September, for both the coast of France and more northern areas (ranging from the UK to Norway/Iceland). However, these descriptive histograms were based on rather small samples ($N = 64$ sightings in total for both areas). They also included sightings of captured turtles, whether these were alive or dead (this was because they were alive at the time of the capture). Furthermore, for the French coast, the pattern of occurrence was unclear, and in the more northerly areas turtles tend to be sighted relatively later in the summer (Brongersma 1972). Overall, differences between the more recent data (Duguy and co-workers, Pierpoint 2000) and Brongersma's work (1972) are thought to have arisen from the factors explained above, and hence are considered to be not significant.

The time lag between the peaks of live sightings and dead strandings strongly suggests that dead strandings and live sightings originate from the same population (i.e. the dead strandings originate from turtles visiting and dying in, or quite nearby, the study area). Brongersma (1972) also noted that, for the Bay of Biscay, dead turtles were found only during months when live turtles were common. The idea that all records are from the same population is corroborated by the fact that, for any one year (1979-2000), the first record of a live sighting always occurred before the first record of a dead stranding. Hence, the time lag between the occurrence of live sightings and dead strandings was likely to be due to the fact that dead (or dying) turtles drift for an indeterminate period before being washed up on shore and then having a chance of being reported (Godley *et al.* 1998).

Causes of mortality for Leatherback turtles in the Bay of Biscay include interactions with fisheries (nets, ropes and trawls) and ingestions of floating waste such as plastic bags (see Duguy *et al.* 1998a, 2000a). With regard to the latter, Leatherback turtles are thought to ingest plastic bags because they mistake them for jellyfish. Indeed, the Leatherback turtle has a highly specialised diet: in the north Atlantic, it feeds almost exclusively on surface-dwelling medusae (jellyfish), although also consuming related animals such as siphonophores, salps and large pyrosomas (Davenport & Wrench 1990, Holland *et al.* 1990, Davenport 1998), which may be found at great depths.

Annual incidences of live sightings and dead strandings were positively correlated, a relationship also shown for the incidences in the UK & Irish waters (Pierpoint 2000). Assuming that live sightings and dead strandings show comparable probabilities of being reported, one may suggest that annual variations in the incidence of dead strandings reflect similar variations in the absolute abundances of live turtles in the area, without necessarily reflecting a certain degree of mortality rate. Generally speaking, the incidence of dead strandings was likely to reflect a combination of the absolute abundance of live turtles visiting the area that year, the mortality rate, and the proportion of dead turtles brought on-shore (which maybe helped by physical factors, such as strong westerly winds) (Duguy *et al.* 1997, Godley *et al.* 1998).

Monthly SSTs and patterns of occurrences of live sightings in the study area

A correlation between the presence/absence of Leatherback turtles in northern Atlantic European waters and SSTs was hypothesised by Brongersma (1972), who noted that live turtles were only observed in waters warmer than about 11°C. He assumed that turtles would actually die in colder SSTs. More recent work suggests that the Leatherback turtle is a facultative endotherm that would be capable of maintaining a core temperature around 25°C in waters of about 5-7°C (Frair *et al.* 1972, Davenport *et al.* 1990, Holland *et al.* 1990, Paladino *et al.* 1990). The Leatherback turtle sometimes forages on pyrosomas, which can be found at 500-800 m during the day (Davenport & Balazs 1991), a depth well within the depth capability of this turtle (Eckert *et al.* 1986). At this depth, the water is cold (5°C is universal when deeper than 1000 m, whatever the latitude, Davenport 1988), and this turtle would maintain a core temperature solely because of the species' large size, good insulation and control of peripheral circulation. This physiological adaptation is termed 'gigantothermy', which basically is endothermy without the enhanced metabolic rate of birds and mammals (Paladino *et al.* 1990).

However, the Leatherback turtle may have a physiological preference (or tolerance) for a given thermal range that would minimise the energetic cost of thermoregulation and endothermy. A preferred thermal niche is likely to be a factor influencing the spatial and temporal patterns of occurrence of live turtles in different areas of the globe throughout the year. In the present study and others studies (Starbird *et al.* 1993, Kenney 1996), it has been reported that the peaks of live sightings usually coincide with the months of warmest SSTs. In Monterey Bay (California), turtles were found to enter the area when SSTs reached a minimum of 15-16°C (Starbird *et al.* 1993), which is consistent with the patterns of occurrence in the Bay of Biscay, where very few live turtles were sighted during months with mean SST less than 16°C. A study on the North-Eastern US coast revealed that 50% of live sightings occurred in waters warmer than 18-23°C, whilst there was a gradual decline in live sightings correlated with declining SSTs (Shoop & Kenney 1992).

Furthermore, the timing of peak sighting occurrences appeared to be latitude-dependent on the US Atlantic coast (see figure 5-6, p. 163, for locations). Indeed, live sightings tend to peak rather early in the year (i.e. March-May) for Georgia (31°N, Dodd & Mackinnon 2000), whilst they tend to peak progressively later on at higher latitudes as the season progresses. For North Carolina (35°N), they tend to peak in May/early June (Epperly *et al.* 1995, Grant *et al.* 1996), and further north in the Gulf of Maine (41°-43°N), they tend to peak in August/September (Prescott 1988, Shoop & Kenney 1992).

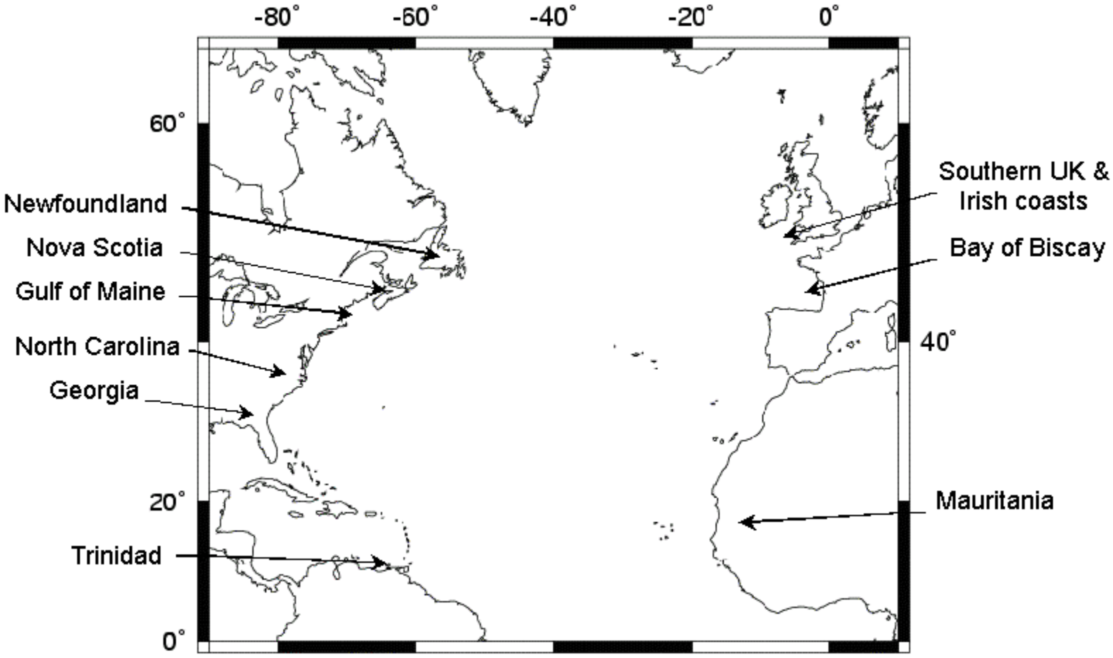
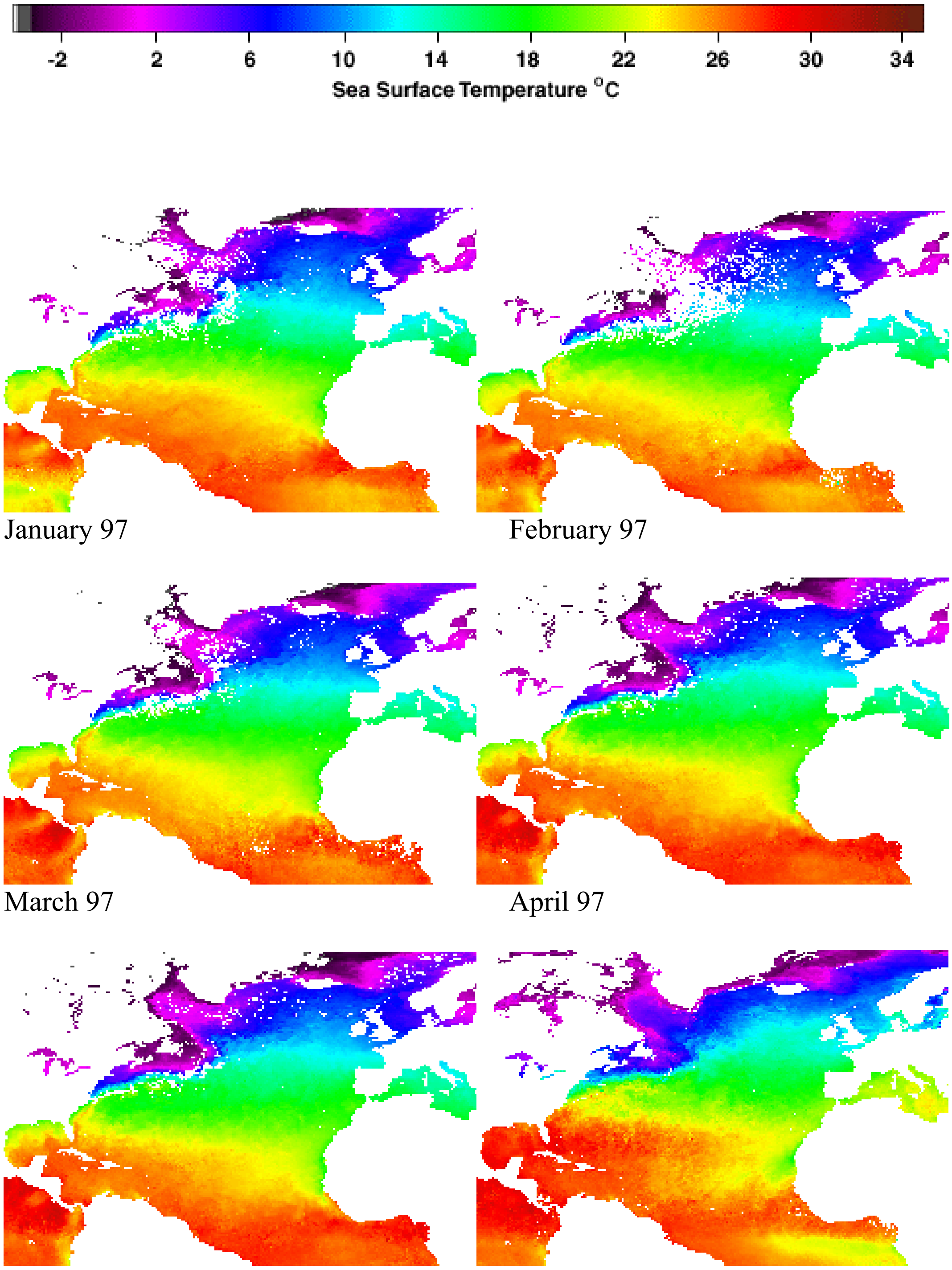


Figure 5-6. Some locations mentioned in the text.

In order to examine, in relation with SSTs, the temporal and spatial patterns of Leatherback turtles occurrence in the northern Atlantic waters, false colour images of SSTs taken by the AVHRRs (Advanced Very High Resolution Radiometer) aboard NOAA polar orbiting satellites, were used for January-December 1997. Images showing monthly averaged data at 54 km resolution were made available by the NOAA/NASA Pathfinder Program (http://podaac.jlp.nasa.gov/SST). This was to get an impression of how SSTs evolve, temporally and spatially, with latitude throughout the year (figure 5-7, p. 165-6, January-December 1997). If the locations where Leatherback turtles were sighted are plotted on the SSTs images corresponding to the months of peak sighting occurrences (figure 5-8 A-C, p. 167), it is found that SSTs tend to be around 18°C at the time of peak occurrences. This is also the case for the month of peak sighting occurrence (i.e. August) for the Bay of Biscay and the southern British and Irish coasts (Pierpoint 2000) (figure 5-8 D, p. 167).

The fact that the peak occurrences of live sightings tend to be associated with SSTs of about 18°C is consistent with the idea of a thermal preference by Leatherback turtles. However, such a preference for a given thermal environment does not allow us to conclude that Leatherback turtles time their migratory movements from tropical waters into temperate waters, and back, solely in the purpose of remaining in waters of at least 18°C. In addition to the metabolic advantage of travelling through warm waters, there could be an alternative motive to their long-distance movements. Indeed, the spatial and temporal distributions of marine animals can reflect variations in their ecological requirements, meaning that prey abundance and movement are very important factors controlling the occurrence, abundance and movement of marine animals (Shoop & Kenney 1992, Weir *et al.* 2001). For instance, Morreale *et al.* (1996) has suggested that the existence of a migration corridor for Leatherback turtles leaving their nesting sites in Costa Rica may result from the distribution and availability of marine resources.

The fact that Leatherback turtles use the north Atlantic European and the north Atlantic US coastal waters as seasonal habitats during the summer months has been linked to the concomitant seasonal high abundance of scyphozoans, their gelatinous foraging material (Davenport & Wrench 1990, Holland *et al.* 1990, Shoop & Kenney 1992). Due to its diet of poor nutritional density based on gelatinous material, the



January 97

February 97

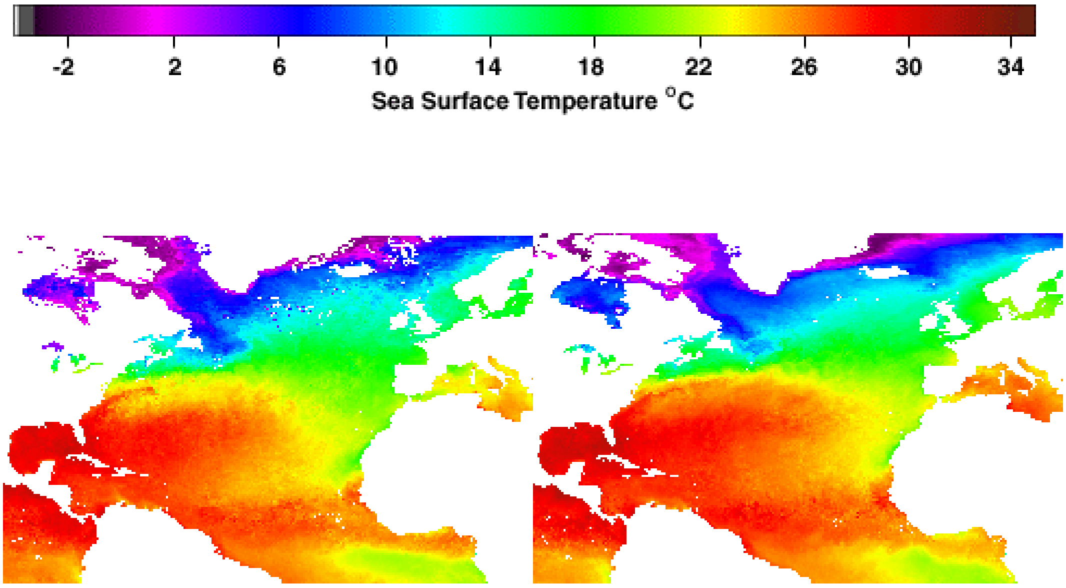
March 97

April 97

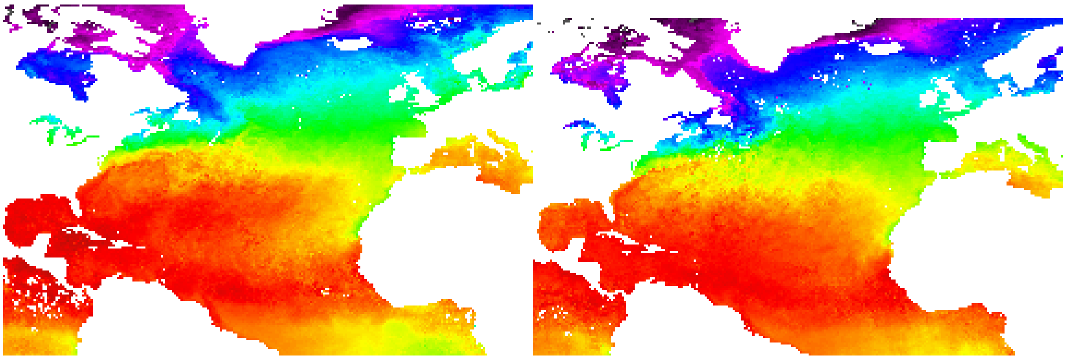
May 97

June 97

Figure 5-7. Monthly Sea Surface Temperatures, January-June 1997



July 97 August 97



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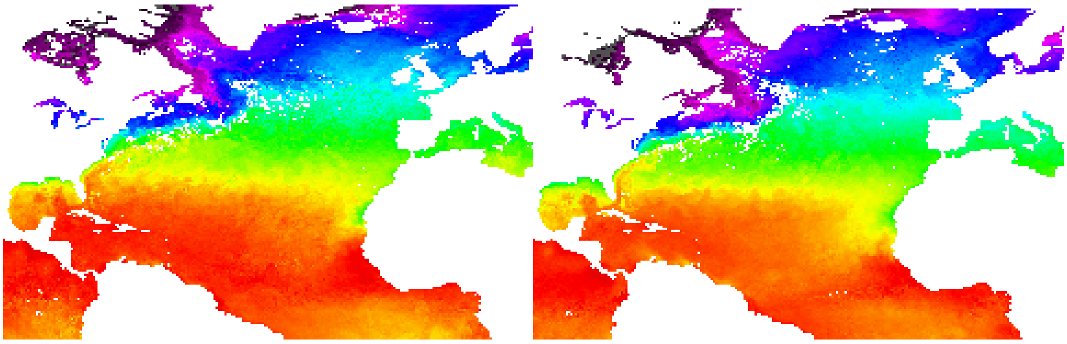

November 97 December 97

Figure 5-7. Monthly Sea Surface Temperatures, July-December 1997

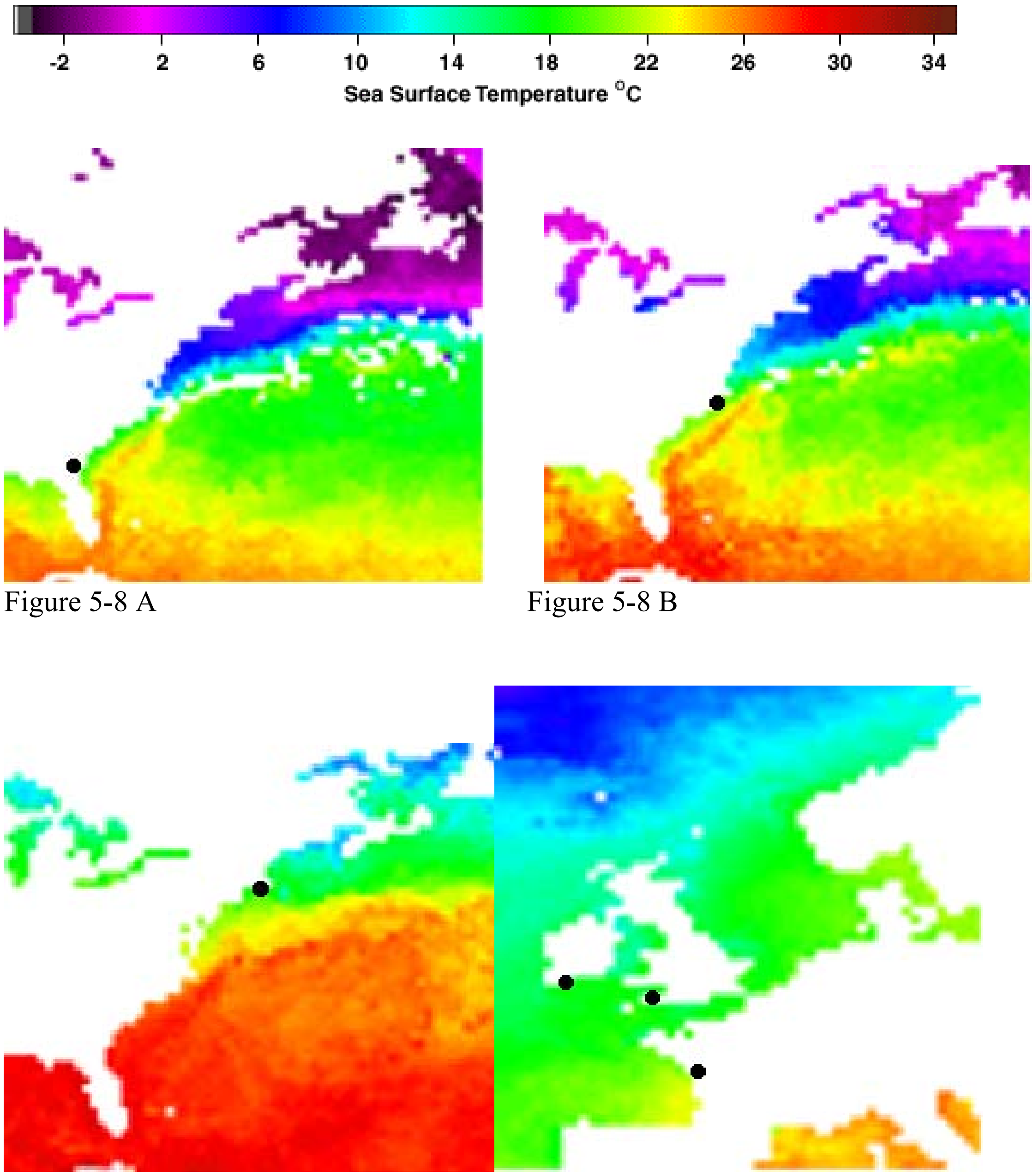

Figure 5-8 A

Figure 5-8 B

Figure 5-8 C

Figure 5-8 D

Figure 5-8. (A) April 1997, peak occurrence of live sightings for 31°N (Georgia, USA). (B) May 1997, peak occurrence of live sightings for 35°N (North Carolina, USA). (C) September 1997, peak occurrence of live sightings for 42°N (Gulf of Maine, USA). (D) August 1997, peak occurrence of live sightings for 46°N (Bay of Biscay, France), 50-54°N (British & Irish southern coasts).

Leatherback turtle needs to ingest vast quantities of jellyfish in order to satisfy its daily energetic requirements (Davenport 1998). Adults can consume as much as 20-30% of their body weight per day, rather than the 3-5% of green and loggerhead turtles (Davenport & Balazs 1991). Such a large-scale foraging activity is made possible by the fact that, when feeding in jellyfish swarms, Leatherback turtles can capture additional prey items whilst continuing to transport food to the oesophagus, in a conveyor-belt-like process (Bels *et al.* 1998).

In fact, the co-occurrence of Leatherback turtles and scyphozoans in near shore temperate waters has been widely reported (Shoop & Kenney 1992, Starbird *et al.* 1993, Kenney 1996, Grant *et al.* 1996). On the North-East US coast, Leatherback turtle and Sunfish (*Mola spp.*) occurrences (Sunfish also feed on scyphozoans) were found to be nearly identical (Shoop & Kenney 1992, Kenney 1996). In the Bay of Biscay, the Leatherback turtle feeds extensively on *Rhizostoma pulmo* (the most common jellyfish of the Pertuis Charentais), whilst also consuming *Chrysaora hysoscella*, *Aurelia aurita*, and more rarely *Cyanea lamarckii* (Duguy 1982). In temperate waters, these scyphozoans present annual cycles, with an alternation between a sexual, medusoid pelagic stage and an asexual polypoid benthic stage (Brodeur *et al.* 1999). The medusae forms generally feeds on zooplankton and shows peaks of abundance in the spring and summer months (the exact timing depends on the species), being extremely rare during the autumn and winter months, except for some large individuals over-wintering in deep waters (Russel 1970). The temporal occurrence of *Rhizostoma pulmo* in the Pertuis Charentais is usually centred on July/August, at which time they reproduce, before their disappearance in September/October. Furthermore, the appearance in May/June of this species of jellyfish has been anecdotally correlated with the first observation of Leatherback turtles in the waters of the Bay of Biscay (Duguy 1982).

Although jellyfish species are present all year round in warm tropical waters, the relatively much greater seasonal abundances of jellyfish during the productive summer months (following the spring blooms of phytoplankton and zooplankton) at higher latitudes may make them worth the trip. This seasonal migration of Leatherback turtles to higher latitudes may therefore satisfy foraging purposes, but ultimately, the warmer SSTs of temperate waters during summer months might also substantially reduce thermoregulatory costs during that period of time. At the end of the productive season in temperate waters, when their foraging material starts to decline (jellyfish are short-lived) and SSTs start decreasing, turtles will then return to warmer tropical waters, where foraging material is found all year round.

In contrast to the migrations towards higher latitudes occurring at the start of the summer, this return migration towards lower latitudes at the end of the productive season may not be as constrained by SST patterns. There is some recent, although unpublished, information regarding the migratory movements of seven Leatherback turtles in the US Atlantic waters (tracks available on the internet at http://www.seaturtle.ca). These turtles, which are thought to have nested in the Caribbean (evidence was obtained from tags carried by two turtles), had been satellite-tagged in the waters near Nova Scotia, Canada (figure 5-6, p. 163). After attachments of the satellite transmitters at the end of the summers (2000, 2001, 2002), these turtles swam either southwards or in a south-east direction, reaching warm tropical waters (around 20°LatN) by November/December.

Long-term trends in the patterns of occurrence of live sightings in the study area

The strong seasonal pattern for the period 1979-2000 was conserved when the dataset from Duguy and co-workers was arranged into eight groups. Overall, there appear to be no detectable change in the timing of Leatherback occurrence in the Bay of Biscay, although this lack of phenological change in timing of occurrence may have resulted from the low resolution of the dataset. The mean day estimated for 1919-1969 (data from Brongersma 1972) was comparable to the means for 1979-2000. There was an exception, however, since the mean day of Leatherback occurrence in 1984 (a year with relatively cold SSTs) occurred relatively later (of around two weeks) than the mean days calculated for the other seven groups. This would be consistent with the idea that SSTs may apply a constraint on the northwards migration of Leatherback turtles into the Bay of Biscay. But overall, finer-scale fluctuations in the timing of the seasonal occurrences of Leatherback turtles in the Bay of Biscay may be more dependent on the timing of the biological cycle of jellyfish in the area, with turtle arrivals coinciding with emerging food resources. Additional studies on resource availability and subsequent exploitation by turtles are needed to better define the habitat characteristics associated with their seasonal patterns of occurrence (Shoop & Kenney 1992). Alternatively, broad-scale effects of climatic fluctuations (e.g. the North Atlantic Oscillation, NAO) may be more important that local temperature for such long-distance migrants as the Leatherback turtle (Huppop & Huppop 2003). For instance, the positive effect of the NAO on Eastern Atlantic sea temperatures (Ottersen *et al.* 2001) may in turn affect gelatinous zooplankton (such cyclic fluctuations in the context of climatic changes are well known, e.g. Brodeur *et al.* 1999). Finally, since jellyfish are dispersed due to ocean currents and tide in addition to wind action near the sea surface (west wind stress is strongly affected by NAO), there is a need for further investigation into any such link between NAO and Leatherback occurrence.

Patterns of occurrence of live sightings, north and south of the study area

The timing and patterns of the migratory behaviours of marine animals can sometimes be studied simply using incidental sightings, since changes in spatial and temporal distributions may reflect migratory patterns. The aim in comparing patterns of Leatherback occurrence in different parts of European Atlantic waters was to try and highlight general patterns of movement, i.e. would the turtles arrive in the Bay of Biscay from the south, from the west, or from both directions? The patterns generated by the data of the present study are actually difficult to interpret in terms of migratory movements, mainly because the seasonal patterns recorded in the UK & Irish waters and Norway is remarkably similar to the patterns in the Bay of Biscay (with incidences of live sightings peaking in August for both areas, Pierpoint 2000), and because of the small samples for the two other areas (north and south of the study area). However, Pierpoint (2000) noted that, in general, Leatherback turtles occurred later in Scottish waters (August-October) than further south (July-September), with turtles probably moving into British and Irish waters from the south and west, before moving northwards, possibly towards Sweden or Norway.

It is known that Leatherback turtles nesting in the Caribbean wander along the Atlantic US coast northwards, and there are some reports of these turtles in the waters near Newfoundland (figure 5-6, p. 163). Brongersma (1972) suggested that instead of turning back to the Caribbean in the Autumn, some could continue their journey by following the Gulf stream and North Atlantic Drift to Europe (Brongersma 1972). Indeed, the Leatherback turtles seen in the Bay of Biscay are generally thought to have migrated either from Africa or/and from the Americas (where they breed and nest). American origin is suggested by the capture and release in the Bay of Biscay, of an adult female previously tagged in French Guiana (5°47’N, 53°55’W) (Fretey & Girondot 1996, Godley *et al.* 1998), and by one satellite-transmitter experiment (Eckert 1998). In the last study, a Leatherback turtle which had nested in Trinidad, West Indies (figure 5-6, p. 163), swam across the Atlantic and then north to the Bay of Biscay. It eventually turned south at the end of November, subsequently arriving 200 km away from the coast of Mauritania (west Africa) by March.

Hence, the Leatherback turtles observed in the Atlantic European waters will turn back to warmer seas in sub-tropical or tropical regions, but do they subsequently go to nesting sites in the Caribbean, or do they move southwards along the coast of Europe and then Africa? The deployment of a few tens of satellite transmitters could, in fact, shed more light on the migratory routes of the Leatherback turtles in the European Atlantic waters, than the compilation of incidental sightings over decades and maybe even centuries.

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