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Speed of travel of migrating Green turtles (*Chelonia mydas*) from Ascension Island to Brazil

By

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To my parents, Valentin and Gloria
To my sisters, Ana and Laura
To my aunt, Dora
To my grandma, Pilar
To my uncle, Arturo
To my best friend, Esther
To all my friends from University in Madrid

But especially… … … to my niece ***Paula*** *to*
whom I dedicate anything I do.

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...6th September 2002...

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

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CONTENTS

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SUMMARY

This thesis investigates the speed of travel during migration from Ascension Island to Brazil of 12 female green sea turtles (*Chelonia mydas*). Diving behaviour (Mean dive duration, standard deviation of the mean dive duration and number of dives), the prevailing oceanic currents (north-south component, east-west component, speed of the current and angle between the direction of the current and the direction of the turtle) and size, were analysed to determine their possible influence on the speed of travel. Two different methods were applied: (1) a detailed analysis made by dividing the migration route into pixels of 1.25 ° longitude x 1.25° latitude and (2) a general study on the overall speed of travel.

The mean speed of travel of migrating Ascension Island green turtles was found to be 2.59 km/h, most likely to be the speed at which the Cost of Transport (COT) is minimal. The speed of migrating turtles from Ascension Island depends on the mean duration of dives, the number of dives and the angle between the direction they follow and that of the prevailing current. The main factor explaining the variation of the speed of travel of Ascension Island turtles is the duration of the dives. Mean dive duration, its standard deviation and number of dives, are related to the size of the turtles.

GENERAL INTRODUCTION

The present thesis is divided into five different chapters.

Chapter 1. This chapter reviews the diving behaviour and physiology of different species of diving animals as they are recorded in the literature. For example, the use of aerobic and anaerobic metabolism during diving, the concept of cost of transport and the implications of body size are considered. The fundamental objectives of the study were to understand the effects of several variables on the speed of travel of migrating green turtles in the context of the specific conditions, which Ascension Island green turtles face when migrating.

Chapter 2. This chapter is a manuscript published in *Animal Behaviour*. My contribution to this work comes from discussions with my supervisor Graeme Hays about the importance of getting good biological information from the locations provided by the Argos location system despite the relatively poor location accuracy. Many of the locations obtained from the satellite were of poor accuracy (classes A and B) and the error in determining the exact location of an individual can lead to an overestimation or underestimation of the distance covered between two successive locations, with the associated consequences on the calculation of the speed of travel between them. The error in estimating the speed of travel was predicted to increase as the distance between two location points decreased, and vice versa. Graeme Hays designed a model, which calculated the minimum distance required between locations in order to get a reliable estimation of the speed. The results were published in *Animal Behaviour*, (2001). I included this paper as a chapter of my thesis because I collaborated in the first steps of the model design, and because I used the result of the model as a method for estimating the speed of travel of the 12 turtles of the present study.

Chapter 3. The specific methodology that I used for estimating the speed of travel is explained in detail in this chapter. I also explain how the values of each variable that was predicted to affect the speed of travel were obtained and transformed, in the purpose of analysing in detail their influence during migration on the speed of travel, and on the overall speed of migration.

Chapter 4. The results of this study are given, including the effect of various variables on the speed of travel. The performance of different individuals is described, as well as the tendencies during migration and the specific variation of speed of travel of different turtles. The results obtained from a green turtle population from Malaysia are compared to the 12 turtles studied from Ascension Island.

Chapter 5. In this chapter, I discuss the relevance of the results obtained, especially the importance of optimising swimming speed during migration. I also clarify the special conditions of this particular population of green turtles compared to findings of other works. The strategies that the turtles should follow are highlighted, as supported by the results. The effects of currents on migration are also discussed, as well as the possible explanation for the differences between Malaysia and Ascension Island populations. Finally, conclusions and recommendations are included in this chapter.

CHAPTER I

Aspects of the physiology and behaviour of diving animals leading to energy conserving strategies

Before starting to analyse the speed of travel of migrating green turtles, I shall consider some aspects of the physiology and behaviour of marine animals. Swimming speed and diving behaviour are variables closely related for many marine animals, such as Rockhopper penguins (*Eudyptes chrysocome moseleyi*) (Cherel *et al* 1999), Bottlenose dolphins (*Tursiops truncates*) (Yazdi *et al* 1999) and several species of cetaceans and pinnipeds (Williams *et al* 2000). These two variables might be fundamental determinants of the metabolic requirements of migrating animals

Efficiency of aerobic and anaerobic metabolisms and aerobic dive limit

As opposed to fish, which extract oxygen from water, some large marine vertebrates such as sea turtles, obtain oxygen directly by breathing in air at the water surface. Consequently, they periodically need to return to the surface to replenish their oxygen stores. Under normal circumstances they will refill their oxygen stores well before they become entirely depleted, so as to avoid the extra costs of anaerobic metabolism (Prange 1976). Aerobic metabolism is more efficient than anaerobic metabolism in producing the energy necessary for body functions (Schmidt-Nielsen 1972). Hence, if under extreme circumstances, animals need to switch to anaerobiosis, the overall metabolic cost of generating energy will be greater. Therefore, diving animals are expected to routinely employ aerobic metabolism. To support this, records from several species show that the great majority of dives performed by free ranging large vertebrates are short and aerobic (Thompson & Fedak 1993). This suggests that the use of anaerobic metabolism is primarily an emergency measure. When necessary, animals can switch to anaerobic metabolism in order to conserve oxygen for important aerobic tissues like the brain and heart (Thompson *et al.* 1993).

Whilst underwater, diving animals can only remain aerobic for a limited amount of time. The amount of time depends on the size of the oxygen stores prior to submergence and on the rate of energy expenditure whilst submerged. The greater the swimming speed, i.e. the greater the activity levels, the greater the rate of energy expenditure. The aerobic dive limit (ADL) is defined as the length of time before which an increase in blood lactic acid concentration occurs (Thompson & Fedak 1993). An increased level of blood lactate after a dive is a sign that the animal has exceeded its ADL, and has started using anaerobic metabolism to cover its metabolic needs. If the energetic cost of swimming increases, the aerobic dive limit will be reduced. Williams *et al.* (1999) suggested that the physiological responses of a diving mammal will be a result of the effects of apnea superimposed on swimming exercise (Castellini et al. 1985; in Williams *et al.* 1999). While one attempts to conserve oxygen, the other utilises it.

Marine animals try to remain aerobic when diving by adopting cost-efficient behaviours (Thompson *et al.* 1993). A significant relationship exists between the swimming speed and the duration of dives, suggesting that short dives would allow the animals to travel faster because of their relatively lower impact on oxygen stores (Williams *et al.* 1996, as quoted in Williams *et al.* 1999) During longer dives, the oxygen availability is reduced and animals tend to adopt energy-conserving strategies.

Aerobic and anaerobic metabolisms in sea turtles

Berkson (1966, in Lutcavage & Lutz 1991) showed that sea turtles are exceptional breath-hold divers. They possess a high anaerobic capacity, and like some freshwater turtles, an anoxic tolerant brain. Despite their large anaerobic capacity, sea turtles are believed to remain aerobic during routine diving. For instance, leatherback sea turtles (*Dermochelys coriacea*) can dive continuously without long recovery periods at the surface (Eckert *et al.* 1986; Standora *et al.* 1984; in Southwood *et al.* 1999), which indicates that leatherback turtles do not normally make use of anaerobic metabolism whilst diving. Similarly, loggerhead turtles (*Caretta caretta*) (Lutcavage & Lutz 1991) and green turtles (Brill *et al.* 1995, Prange 1976) were found to routinely dive aerobically. If green turtles (*Chelonia mydas*) routinely dive aerobically (Prange 1976), it seems logical that they would do so during migration. Indeed, during that time they have access to oxygen, from which to derive part of the energy necessary to swim. Besides, using aerobic metabolism instead of anaerobic metabolism would help them to conserve their limited energy reserves (Carr & Goodman 1970). The efficient ventilatory patterns of loggerhead and other sea turtles result from their highly elastic and reinforced lungs and from their high pulmonary oxygen diffusion capability (Lutcavage & Lutz 1991). Their highly adapted lungs allow sea turtles to reduce the time spent at the surface for loading up oxygen (Lutcavage *et al* 1987).

Another diving reptile, the sea snake, *Pelamis platurus*, prevents switching from an aerobic to an anaerobic metabolism by reducing its metabolic rate and/or by increasing the rate of cutaneous oxygen uptake. This allows it to dive continuously, without long recovery surface intervals. Nevertheless, non-physiological factors can also influence their behaviour in the water. For example, surface conditions and subsurface temperatures have been shown to significantly influence their diving behaviour, highlighting the necessity of considering both physical and physiological factors when studying the behaviour of marine animals (Rubinoff *et al.* 1986).

Circulatory changes during diving

Some diving animals can make use of bradycardia in order to remain aerobic as long as possible. Bradycardia is a decrease of the heart rate and it is one of the most characteristic physiological responses observed in diving animals. There is a sudden drop in heart rate at the beginning of submersion that must be caused by a nerve reflex, for if it were a response to a gradual depletion of oxygen, it would develop more slowly (Schmidt-Nielsen, 1997). Bottlenose dolphins present a rapid bradycardia upon submergence (Williams *et al.* 1999). Also their heart rate increases during the first minute after submergence and is correlated with dive depth and duration. Similar patterns for heart rate have been reported for swimming and diving white whales (Williams *et al* 1999). In these studies, the blood concentration in lactate increased with dive depth and differed significantly once depth exceeded 140 m, suggesting that the animals had exceeded their aerobic dive limit. Williams *et al.* (1999) suggested that the duration of submergence, rather than the level of exercise *per se*, was the cause of the changes in heart rates and respiration levels in bottlenose dolphins.

Extreme bradycardia (Thompson & Fedak 1993) has also been reported in grey seals (*Halichoerus grypus*). High post-surfacing blood lactate levels were recorded as well as extended recovery periods at the surface, the latter being an indication of a switch to anaerobic metabolism. Changes in heart rate during diving have also been observed by Thompson & Fedak (1993) for grey seals: heart rates were high and rhythmic at the surface, with the presence of a pre-surfacing tachycardia and of an intensification of bradycardia with increased dive duration. Heart rates were also arrhythmic during longer dives, with the presence of long pauses between heart beats. In addition, the surface heart rate was significantly related to the size of the animal. Many air-breathing aquatic animals, such as penguins (Adélie: Culik 1992, Culik *et al.* 1994, Emperor: Kooyman *et al.* 1992, Culik 1994, and King: Culik *et al.* 1996) have been shown to reduce their heart rate after submersion.

Oxygen stores and cardio-respiratory adjustments during diving

The green turtles have been observed pronounced reductions in heart rate and cardiac output during submergence (Berkson 1966, in Brill *et al.* 1995). Since sea turtles are reptiles, their diving behaviour might differ from the behaviours adopted by birds and mammals. However, similarly to mammals, the brain and heart are the main organs towards which oxygen is directed, to the detriment of other more peripheral organs that are less crucial to the survival of the individual. In the green turtle, the lungs will remain well supplied with oxygen because they are the main oxygen store (Prange & Jackson 1976; Lapennas & Lutz 1982; Lutz & Bentley 1985, in Brill *et al.* 1995). Lutcavage *et al.* (1987)

observed that the loggerhead sea turtle had almost fully saturated blood prior to a dive as an additional way to store oxygen prior to submergence.

Similarly, Lutcavage *et al.* (1992, as quoted in Southwood *et al.* 1999) observed that leatherback turtles use their blood and tissues as their main oxygen store, instead of their lungs (as in the green and loggerhead turtles). This facilitates the availability of oxygen when the lungs collapse under increased hydrostatic pressure at great depths. The utilisation of blood oxygen stores is controlled by cardiovascular adjustments. For instance, increases in heart rate and tissue perfusion upon surfacing facilitates the exchange of gases and reduces the amount of time necessary to reload oxygen stores, thus shortening the recovery surface intervals. Heart rate of leatherback turtles has been shown to decrease immediately upon submergence, continuing to fall during the descent portion of the dive. During the ascent portion of the dive, leatherback turtles displayed an increase in heart rate. Upon submergence, a decrease in heart rate would result in a slower delivery of oxygen to the tissues conserving oxygen during diving (Southwood *et al.* 1999).

Temperature regulation in diving animals

Although sea turtles are not endothermic animals, it remains interesting to know how endotherms manage to cover their thermoregulatory costs. For instance, swimming Humboldt penguins (*Spheniscus humboldti*) go back on land at night if the water temperature is very low, because the thermoregulatory cost of staying on the water is greater than the one in the air. The energetic cost of leaving and returning to the sea remains less than the one of remaining in the water (Luna-Jorkera & Culik 2000).

Bottlenose dolphins can decrease their thermoregulatory costs by using the heat generated by their locomotor action. (Yazdi *et al.* 1999). When swimming, the overall metabolic rate will be the sum of (1) the increasing power used to overcome hydrodynamic drag and of (2) the thermoregulatory costs, which are lowered because of locomotion action. They stated that this theory can be applied to swimming homeotherms from the 4 kg Adelie penguin to the 4000 kg Minke whale. Hind & Gurney (1997) used the seal as an example to describe the metabolic cost homeotherms face when swimming. In order to maintain a constant core temperature, seals must increase their metabolic rate. The cost of thermoregulation decreases as the seals progressively swim faster, the waste heat from locomotion compensating for the heat loss. When the heat generated from basal metabolism and locomotion exceeds the minimum heat loss, total metabolic rate increases exactly in proportion to the mechanical costs of locomotion. This suggests that there is a range of swimming speeds optimum for the animal in terms of minimising the metabolic cost of swimming.

Lutcavage & Lutz (1991) reported that in loggerhead turtles, both activity levels and temperature increase the metabolic rate. Also Southwood *et al.* (1999) suggested that long surface intervals might also play a role in temperature regulation in the leatherback turtle. Paladino *et al.* (1990) named "gigantothermy" the ability of Leatherback turtles to maintain high body temperatures (around 25°C) in cold water (around 7°C) by large body size, low metabolic rate, and use of peripheral tissues as insulation. Large dinosaurs could have used this thermoregulatory adaptation of large animals for thermoregulatory purposes.

Energy-conserving diving behaviours: gliding and depth of dives

Williams *et al.* (2000) compared the behaviour of four species of marine mammals, by assessing the wide variety of energy-conserving swimming behaviours that they have developed to reduce the cost of swimming. Despite the differences between species (differences independent of evolution, body size, and propulsive mechanism), the authors found that marine animals have developed similar behaviours in order to use energy more efficiently. For instance, gliding is one of such common behaviours. Gliding started at similar depths for both seals and dolphins, and changes in hydrostatic pressure and buoyant forces might be the cause of such similarity in behaviour. More generally, marine animals reduce their locomotor effort by gliding, hence decreasing their overall energy expenditure. In addition to the above, Williams *et al.* (1999) found that diving Bottlenose dolphins presented long periods of gliding accompanied by interrupted patterns of propulsion. Such a locomotor pattern and the absence of muscular effort during extended glides promote energy savings, allowing the animals to increase their time under water. Williams *et al.* (1999) also suggested that changes in buoyancy and swimming strategy provide an important opportunity to minimise energy cost at depth.

Williams *et al* (2000) stated that greater energy savings generally occurred during deeper dives (which is consistent with the increase in the proportion of time gliding). The authors also suggested that energetic savings of submerged swimming might reduce the cost of long-distance migrations. An optimum submerged swimming strategy would probably favour the conservation of the limited energy stores during migration of the green turtle.

Implications of body size

Large animals usually dive longer than smaller animals of similar design. This is because there is a more favourable relationship between the size of the oxygen stores and the mass-specific metabolic rate in larger animals (Schreer & Kovacs 1997, in Southwood *et al.* 1999). Maximum dive depth, maximum dive duration and dive angles are dependent on the size of the individuals for several penguin species: larger species perform longer and deeper dives than smaller ones (Culik *et al.* 1996; Putz *et al.* 1998; Cherel *et al.* 1999; Radl & Culik 1999). Culik *et al.* (1996) also suggested that the correlation between size and dive performance should also be valid intra-specifically, as well as between species. A similar relationship between body size and diving behaviour has also been observed for Antarctic fur seals: there was a different distribution of dive depths between sexes as a result of the difference in size between male and female individuals (Boyd *et al.* 1998).

In the leatherback sea turtle, body size (measured as curved carapace length or CCL) correlates significantly with dive depth, dive duration and surface intervals (Southwood *et al.* 1999). Leatherback turtles present some features, such as their large size (250-600 kg) and their capacity to maintain high core body temperatures in cold water (Friar *et al.* 1972, in Southwood *et al.* 1999), which are similar to those of mammals. However, when these turtles are compared with mammals of similar sizes, some differences arise. For instance, dives performed by leatherbacks are shorter and the surface time between dives is longer than for similarly sized mammals.

When swimming speed is viewed in the light of body size, there is a tendency for larger species to swim faster than smaller species (Putz *et al.* 1998). For example, king penguins swim at a relatively high underwater speed, approximately 10% higher that those of "non-aptenodytes" penguins (aptenodytes are the largest penguins: King and Emperor penguins). On the other hand, swimming speeds of little penguins are considerably lower than those of larger penguin species. Because of their small size, little penguins have high-energy requirements for swimming as compared to other bigger penguins (Bethge *et al.* 1997).

Oxygen stores and metabolic rates are also size-related: a bigger animal will have greater oxygen stores than a smaller animal, but its mass-specific metabolic rate will be less than the one of a smaller animal (Butler & Jones 1982, as quoted in Lutcavage & Lutz 1991). Therefore, larger species can afford to swim faster than smaller ones. However, larger species will also have higher absolute energy requirements (Mate *et al.* 1999).

In order to maintain a constant swimming speed, an animal must balance the drag forces resulting from its forward movement in the water with the thrust force generated by its swimming action. The amplitude of the drag force acting on the animal is directly dependent on the size of the individual, its shape and its swimming speed, as well as on the physical properties of the water (Hind & Gurney 1997).

The Energetic costs of swimming

As mentioned already, animals can use oxygen more efficiently by modifying the duration and the depth of their dives as well as their swimming speed. The rate of energy expenditure during a dive is proportional to the rate of oxygen consumption, which is a function of the swimming speed (Thompson *et al.* 1993). For instance, the overall rate of prey encounter depends on the swimming speed (Culik *et al.* 1994; Radl & Culik 1999). Hunting animals should therefore swim at speeds that maximise the energy gained (via hunting) per unit of energy expended (via the swimming action) (Thompson *et al.* 1993). If the cost of a dive is small compared to the gain per encounter, the net energy gain is maximised by swimming faster than the prey.

The oxygen consumption of marine animals increases with swimming speed. At a maximum swimming speed, oxygen consumption was between three and four times greater than the resting levels for juvenile green turtles swimming in a water flume (Prange 1976). As mentioned already, the green turtles nesting at Ascension Island are believed not to feed during their migration from Brazil to Ascension and back. Prange (1976) calculated the amount of fat reserves that an adult green turtle would utilise if it swam at its maximum speed (estimated of approximately 7.2 km/h) instead of adopting a slower but more economical swimming speed. Under such circumstances, the distance would be covered in only 667 h (instead of much longer), but the migration would require a stored fat reserve equivalent to more than three times the body mass of the turtle. This example shows the relevance of travelling at a speed that minimises the cost of transport as opposed to the maximum swimming speed in terms of energy expenditure and saving. The optimal swimming speed is determined by several factors, and one of them is the amount of energy that the individual can allocate to locomotion.

It can be extrapolated from the preceding that animals will try to stay within their ADL whilst diving by using physiological and behavioural strategies, so as to avoid the extra cost of anaerobiosis. But, when examining metabolic cost, one more important factor must be taken into account: the cost of transport (COT) of the animal when swimming. The cost of transport is the amount of energy (in Joules) required to transport 1 kg of body mass over a distance of 1 m. Videler & Nolet (1990) suggested that it can also be expressed as divided by the earth acceleration, but this is not commonly used. In order to calculate the cost of transport ($J.kg^{-1}.m^{-1}$) of an animal, the mass-specific power input (or the amount of energy per unit of time, in $J.kg^{-1}.sec^{-1}$) expended during swimming is divided by the swimming speed. The total power input is the metabolic rate of the animal, and increases with swimming speed (Culik *et al.* 1994).

Animals are not expected to swim at the lowest possible speed, but rather at the speed that minimises the overall energy expenditure. For instance, Thompson *et al.* (1993) showed that vertically diving seals should swim at their speed of minimum cost of transport (MCT), then forage at the speed providing the greatest energy gain per unit expanded. Such a strategy would allow these seals to maximise their efficiency of energy utilisation. Swimming speeds slower than the speed of MCT present a rapidly increasing cost of transport. Conversely, at speeds faster than the speed of MCT, the energetic cost of transport increases much more slowly. Thompson *et al.* (1993) predict that when seals are hunting some relatively stationary or very slow-moving prey, seals will maximise the number of encounters per dive if they swim at a speed close to their speed of MCT. Conversely, when hunting more active prey, seals will increase the number of encounters per dive by swimming slower than their speed of MCT, hence reducing their overall swimming activity.

The speed of MCT is size-dependent (see examples in table 1.1 at page 17). The resting metabolic rate of a large animal is lower than that of a smaller animal. Videler & Nolet (1990) showed that, for fish, this difference gradually disappears, as swimming speeds increase. They explained that the decrease in cost of transport with mass was a consequence of the higher optimum swimming speeds of larger animals. Moreover, the cost of locomotion is lower for swimming than for flying and running. Also for swimming animals, the cost of swimming at the surface is much greater than the cost of swimming deeply submerged because a lot of energy is dissipated in the generation of surface waves. (Videler & Nolet 1990). Fish are the animals with the lowest COT (Tucker 1970, Schmidt-Nielsen 1972, as quoted in Prange 1976). However, fish face a lower oxygen availability compared with other diving animals, such as big marine vertebrates.

Prange (1976) showed that green turtles have relatively low costs of transport. Videler & Nolet (1990) compared the optimum speeds of travel (or Uopt, the speed at which the COT is minimal) of several species. They concluded that fish and sea turtles were the species consuming the least energy when swimming at their optimum swimming speed. These animals used up to 5.5 times less energy than the other submerged swimmers. In addition, Prange (1976) reported that the MCT of the green sea turtles was slightly less than that for flying birds, but twice as great as that for fish of similar body mass. He also found that the MCT of hatchlings occurred when hatchlings swam at 75% of their maximum swimming speed. Prange (1976) also suggested that there is a limit for the swimming speed of green turtles, and this maximum swimming speed could be related to their body length.

Ascension Island population of green sea turtles

The aim of this thesis is to study the travelling speed of the green sea turtle of Ascension Island. Green turtles of this specific population migrate relatively long distances between their feeding grounds close to Brazil (between 5 and 10° S, and around 35° W) and their breeding and nesting grounds on Ascension Island (7° 57'S, 14° 22' W). During migration they are predicted to swim within a narrow optimum range of travelling speeds, for which the COT is minimal. The present study attempts to clarify the physiological and surrounding physical factors that drive the free-ranging behaviour of these animals. To achieve this aim, the travelling behaviour of other marine animals has also been reviewed in this chapter.

If the energetic demands of long-distance migration are very high, the physiology and behaviour of green turtles may have evolved to lead to an optimum performance, which would allow these reptiles to efficiently use their energy stores. By identifying the objectives and needs of migrating green turtles (Thompson and Fedak 1993), we will try to clarify the optimal strategy they should adopt. Animals are expected to follow a strategy to maximise their energy efficiency (Welham & Ydenberg 1988, as quoted in Thompson *et al.* 1993). Indeed, for green turtles to successfully reach their destination, a strategy that minimises the cost of transport could be followed, as it will maximise the efficiency of energy utilisation.

Green turtles are believed to fast during migration and at Ascension Island. Although it is possible that they might occasionally feed on an alternative source of food, this species feeds mainly on seagrass, macroalgae, or both (Carr *et al.* 1974; Mortimer & Carr 1987), which are food sources typical of shallow depths close to the coasts that have not been found around the island. If this premise is true, their energy stores will be limited and their performance will thus be determined by the amount of energy they hold and the way they utilise it. Under extreme circumstances (e.g. when their energy reserves have become low), the main objective may become to remain alive. It appears logical that migrating animals would want to minimise the duration of their migration. However, Southwood *et al.* (1999) suggested that for an animal that relies on limited energy reserves, the total energy requirement for a migration might be more important than the time involved. We can hypothesise that the animal will travel at an optimum speed that minimises its COT.

Table 1.1. Differences between Body mass (kg), Speed (km/h) at which the COT is minimal (Uopt), travel speed of animals in the wild of several diving species (km/h), and reference in the bibliography.

Species	Mass(kg)	Travel speed (km/h)	Uopt (km/h)	Reference
Humboldt penguins	3.6	3.24 - 7.19	6.12	41
King penguins	10.1	10.43	7.92	22, 68
Rockhopper penguins	2.3	7.55	-	19
Magellanic penguins	4	5.39	-	69
Adelie penguins	4	-	7.92	21, 7
Chinstrap penguins	3.8	-	8.64	21, 7
Gentoo penguins	5.5	-	6.48	21, 7
Little penguins	1.2	6.47	6.48	7
Grey seals	210	-	4.68	78
Grey seals	155	3.13 - 4.17	-	52
Anctartic fur seals	159	1.44 - 3.59	-	9
Humpback whales	-	3.8	-	50
Right whales	-	2.7	-	50
Gray whale	15,000	4 - 5.1	-	50
Blue Whales	-	4.5	-	51
Bottlenose dolphins	97.5	6.11	6.12 - 8	85, 86

CHAPTER II

The implications of location accuracy for the interpretation of satellite tracking data

The present chapter is a paper published in *Animal Behaviour* that was written by the first author, Dr Graeme Hays. The rest of the authors are cited by alphabetic order.

Hays, G.C., Åkesson, S., Godley, G.J., Luschi, P. and Santidrián, P. 2001. The implications of location accuracy for the interpretation of satellite-tracking data. *Animal Behaviour*, 61: 1035-1040.

Introduction

Over the last two decades, satellite tracking using the Argos system has become a widely used tool, enabling the movements of a large variety of terrestrial, aquatic, and aerial vertebrates to be recorded (e.g. Weimerskirch et al. 1992; Gudmundsson et al. 1995; McConnell & Fedak 1996; Morreale et al. 1996; Block et al. 1998; Boyd 1999; Polovina et al. 2000). Today, the Argos system remains the most widely used tracking method that provides global coverage and, as a consequence, the list of satellite tracking studies grows ever larger. The system uses transmitters (termed platform terminal transmitters or PTTs) that periodically (typically at an interval of around 60 seconds) send a short (typical 360-920 ms) radio signal (401.650 mHz), termed an uplink, to polar-orbiting NOAA satellites. The location of the transmitter is then calculated 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, with each location being assigned a level of accuracy.

A frequent use of satellite tracking is to document long-distance animal movements of hundreds or even thousands of km. When plotting tracks over such spatial scales and describing the general pattern of movement, the inaccuracy of individual locations may be unimportant (e.g. Kjellén et al. 1997). However, once more detailed aspects of Argos tracking data are considered, such as the speed of travel or small scale movements, then location accuracy is likely to become a much more important issue. For example, the speed of travel may be determined be dividing the distance between two Argos locations by the intervening time interval, but this calculation will be compromised if this distance is short and the location inaccuracy is high. Such problems may be particularly acute in marine studies where the diving behaviour of animals can severely limit the number of uplinks received on each satellite overpass and hence a high proportion of locations may be of low quality (e.g. Plotkin 1998). It is, therefore, surprising that the implications of location accuracy, while frequently acknowledged (e.g. Renaud & Carpenter 1994), are rarely considered in detail. Either of two simple filtering processes are generally used to remove "erroneous" locations. First, when there are frequent locations of good accuracy, then poor quality locations may simply be removed from the analysis (e.g. Gudmundsson et al. 1995; Boyd et al. 1998; Klomp & Schultz 2000). This is a valid procedure, but can clearly only be used in studies where good quality locations are obtained frequently. Second, "erroneous" locations may be removed because they necessitate an unrealistically high speed of travel from adjacent locations (e.g. McConnell et al. 1992; McConnell & Fedak 1996; Luschi et al. 1996; Hull et al. 1997; Catard et al. 2000). Again this approach is useful in removing the most erroneous locations. However, the problem here is that many of the calculated speeds, while "biologically realistic", may still be inaccurate.

Given that the Argos system will continue to be widely used by biologists for the foreseeable future, it is important to develop analytical techniques that allow more robust information to be derived from the raw data. Here we critically examine the implications of Argos location accuracy for determining an animal's speed of travel. We develop some simple guidelines for the interpretation of Argos data that will have wide utility regardless of the species under study. Next we implement these guidelines using Argos data for a green turtle swimming across the South Atlantic and show how appropriate data analysis reveals systematic changes in the speed of travel during migration.

General Considerations

Argos assigns a quality index (termed the location class or LC) to each location. Since 1994, locations have been designated as LC 3, 2, 1, 0, A or B. Of these LC 3, 2, 1, and 0 may be provided only when at least 4 uplinks are received on an overpass; LC A occurs when a location is determined from 3 uplinks; and LC B when a location is determined from 2 uplinks. Argos state that the estimated accuracy in latitude and longitude is < 150 m for LC 3, between 150m and 350 m for LC 2, between 350m and 1000m for LC 1 and > 1000m for LC 0 (Argos 1996). While the exact terminology used by Argos has changed slightly between different versions of the user manual (e.g. Argos 1989, 1996), it is generally assumed that location errors follow a bivariate normal distribution around the true position, with the standard deviation of latitudinal location error (σ_x) equalling the standard deviation of longitudinal location error (σ_y) such that for LC 3, $\sigma_x = 150$ m $= \sigma_y$; for LC 2, $\sigma_x = 350$ m $= \sigma_y$; and for LC 1, $\sigma_x = 1000$ m $= \sigma_y$ (Keating 1991). Argos is unable to assign a level of accuracy to LCs A and B.

In general terms, as the distance between two points (d_n) increases and/or the location accuracy (σ, where $\sigma = \sigma_x = \sigma_y$) improves, then the error on the calculated speed of travel will be reduced. To illustrate this effect we assumed that an animal travelled in a straight-line at 2.5 km.h^{-1}. We then randomly selected two positions between 0 and 400 km apart on the true course of the animal. To each of these positions we added a location error randomly selected using different levels of location accuracy (σ) and then calculated the speed of travel between the resulting locations. The same level of location accuracy was used for each pair of locations and for each level, 40,000 simulations of speed of travel were run.

These simulations clearly show the general pattern for the variation in the calculated speed of travel to decrease as both (i) the distance between locations increases and (ii) the location accuracy improves (Fig. 2.1). For σ values of 150m, 350m and 1000m (i.e. corresponding to LCs 3, 2 and 1), the 95% confidence interval on the calculated speed of travel was between 2.25 and 2.75 km. h^{-1} (i.e. the true value + or - 10 %), when the distance between consecutive locations was >3, 5 and 12 km, respectively.

We can extend this analysis, to consider the minimum distance (d_{min}) that is required between two locations to attain this level of accuracy for the calculated speed of travel (i.e. 95% of values lying within the true value + or - 10 %) for other levels of location accuracy. For example, when $\sigma = 2000$ m, $d_{min} = 23$ km, when $\sigma = 5000$ m, $d_{min} = 56$ km and when $\sigma = 10000$m, $d_{min} = 110$ km (Fig. 2.2).

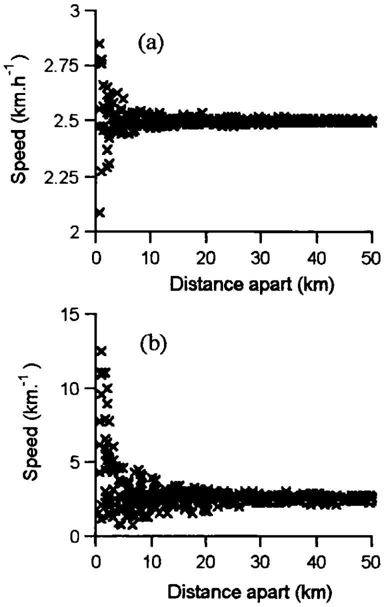

Figure 2.1 The calculated speed of travel as a function of the distance apart of two locations, for an animal moving at a constant 2.5 km.h^{-1}. For each graph, a sample of 500 points are shown (to prevent the plot becoming too cluttered) from a total of 40,000 simulations. (a) $\sigma = 150$ m (i.e. corresponding to LC 3), (b) $\sigma = 5000$ m (this value selected simply to clearly illustrate the affect of different levels of σ).

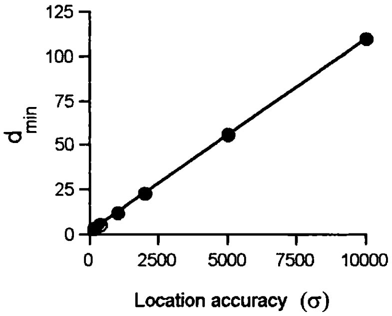

Figure 2.2. For different levels of location accuracy (σ), the minimum distance between two Argos locations (d_{min}) that is required to ensure that the calculated speed of travel lies with 10% of the true values on 95% of occasions. Simulations were run at σ = 150, 350, 1000, 2000, 5000 and 10000. d_{min} (in metres) = 0.0109σ (in metres) + 1.27 ($r^2 = 1.0$)

Direct determination of location accuracy

To directly determine the accuracy of different classes of Argos location, we left PTTs switched on in fixed positions during fieldwork in 1997, 1998, 1999 and 2000 in Brazil (n = 1 PTT switched on for 16 days) and at Ascension Island (n = 8 different PTTs switched on for a total of 15 days). PTTs were Telonics models ST-10 and ST-14 (Telonics, Arizona, USA), models that we have routinely used to track turtles in various studies around the world. The true position of the PTT in each trial was calculated as the mean position of the class 3 locations.

These trials show the general pattern of decreasing accuracy moving from LC 3 to LC B (Table 2.1). The accuracies of location classes 3, 2 and 1 correspond approximately with those detailed by Argos, although σ_y was always greater than σ_x. Such a difference has been reported before (Keating et al. 1991) and suggests that the performance levels reported by Argos may need to be re-evaluated. However, the absolute difference between the performance levels given by Argos and those measured here is small and does not affect our subsequent analysis. Much more important for many animal tracking studies are the accuracies of LC A and LC B, since these accuracies are not reported by Argos. In our trials the accuracy of LC A was comparable to that of LC 1. LC B had poorer accuracy than LC A, but the worst level of accuracy was found in LC 0.

Table 2.1. For each location class (LC), the number of locations obtained when transmitters were in a fixed location, values for σ_x and σ_y and the mean (and SD) deviation of locations from the true position.

LC	n locations	σ_x (km)	σ_y (km)	mean deviation (and SD) in km
3	38	0.12	0.32	0.27 (0.20)
2	28	0.28	0.62	0.54 (0.40)
1	19	1.03	1.62	1.33 (1.35)
0	9	4.29	15.02	10.10 (12.31)
A	18	1.39	0.81	0.99 (1.36)
B	22	5.23	7.79	7.00 (6.92)

Case study: deriving accurate speeds of travel for a migrating green turtle

To consider how knowledge of the interaction between location accuracy and the distance between locations can be used to improve the information derived from Argos tracking, we considered, as an example, real data for a green turtle migrating between Ascension Island and Brazil. This turtle was observed nesting on Ascension Island on the night of 1-2 June 1998. After egg laying was complete, a Telonics ST-10 PTT was attached to the head of the turtle using quick setting epoxy. The last uplink was received from the transmitter 80 days later on 21 August. To date, this is the longest period a transmitter has remained functioning on an Ascension Island turtle and is the only turtle for which we have repeated locations both during the migration to Brazil and in the Brazilian coastal zone. Hence, of the turtles we have tracked from Ascension, this individual is the most appropriate for illustrating our approach for analysis of Argos data.

The study animal began to move away from Ascension Island on 4 June and arrived within 10 km of the coast of Brazil on 11 July. The turtle then travelled along the Brazilian coast until 20 July when its generally southerly coastal travel ceased and it remained in a restricted area until 21 August when the transmitter failed (Fig. 2.3). During the 80 days for which the transmitter functioned, a total of 268 locations were obtained.

In order to rigorously examine the speed of travel during the trans-Atlantic crossing and the subsequent southerly coastal travel, we first conducted an initial data screening. In this screening we removed locations of LC 0 (based on the fact that LC 0 provided the poorest accuracy) (n = 17); locations prior to the departure from Ascension Island (n = 3); locations after the southerly travel along the Brazilian coast had ended (n = 62); locations during the trans-Atlantic crossing that were clearly visibly anomalous (the anomalous nature of these locations was confirmed by all such locations necessitating a speed of travel of ≥ 13 km.h^{-1} (n = 7) which is unrealistically high for turtles); and a location during the period of southerly coastal travel that was well inland. The data-set for subsequent speed of travel analysis therefore had 178 locations (Fig. 2.3b), most of which were LC B (for LC 3, 2, 1, A, and B, n = 1, 5, 14, 53 and 105 respectively) for which we had measured values of σ_x = 5.23 km and σ_y = 7.79 km. The equation in the legend to Fig. 2.2, suggests that a minimum distance of around 86 km is required to obtain accurate estimates of speed of travel from such locations. Erring on the side of caution, we calculated the speed of travel using pairs of locations that were at least 90 km apart. Indeed as some of the locations used were of LC 2, 1 and A, which all had better accuracy than LC B, using locations with a minimum separation of 90 km was even more conservative. We automated the calculations using a macro written in Minitab (Minitab Inc., Pennsylvania, USA). In short, this macro started with the first location (loc-a_1) obtained during migration and then searched through all subsequent locations until the next location ≥ 90 km away was found (loc-b_1). The speed of travel between these two locations was then determined by simply dividing their distance apart in (km) by the intervening time interval (hours). This same location (loc-b_1) was then never used again as the second location of a pair in the speed of travel calculation. In this way consecutive values for speed of travel were calculated independently. For the second location obtained during migration (loc-a_2), the procedure was repeated, and so on. Speeds of travel were subsequently discounted if the straightness index (calculated as the direct distance between locations loc-a_n and loc-b_n divided by the sum of the distances between all the intermediate locations, i.e. (loc-a_1 to loc-a_2) + (loc-a_2 to loc-a_3) + ... (loc-b_{n-1} to loc-b_n) was < 0.88. Consequently any effect on the calculated speed of travel of the turtle not travelling in a straight line was relatively minor.

So what are the effects of this analytical procedure? When the speed of travel is calculated using all consecutive locations, there is great variability in the calculated speeds, with some up to almost 20 $km.h^{-1}$, which is biologically unrealistic (Fig. 2.4a). Also there is no autocorrelation between consecutive speeds (Fig. 2.4b). High speeds of travel may simply be removed from the data. For example we have previously used 5 $km.h^{-1}$ as the upper threshold for inclusion of speeds in subsequent analysis (e.g. Luschi et al. 1998). If such high speeds of travel are removed, considerable variation remains in the data-set (Fig. 2.4c) but a low level of autocorrelation appears between consecutive speeds (Fig. 2.4d). However, once the full data analysis is implemented, using only locations ≥ 90 km apart to determine speed, then clear patterns emerge (Fig. 2.4e). For example, between about 22-27 °W there was a general decline in the speed of travel, while between about 27-34 °W there a general increase. These systematic changes are also shown clearly when the autocorrelation between consecutive speeds of travel is plotted (Fig. 2.4f). Once the turtle arrived at Brazil and travelled southward along the Brazilian coast, its speed of travel showed a clear decrease.

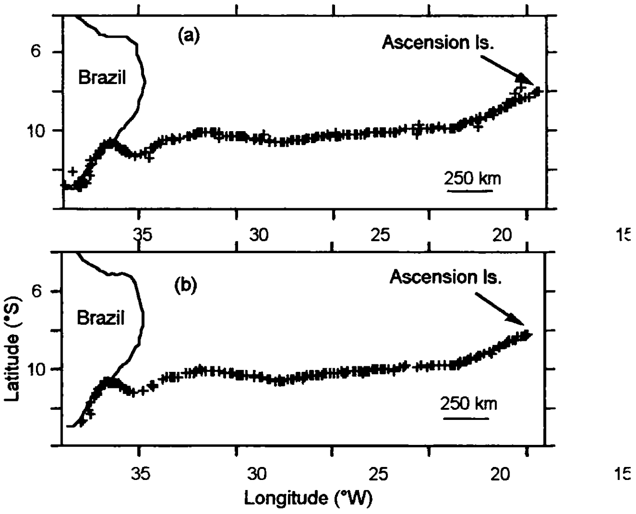

Figure 2.3. (a) All the locations obtained after a transmitter was attached to a nesting female green turtle at Ascension Island. Locations clearly reveal the pattern of westward travel to Brazil, followed by southerly travel along the coast of Brazil. (b) After the initial data screening (see text for details), the 178 locations used in subsequent speed of travel calculations.

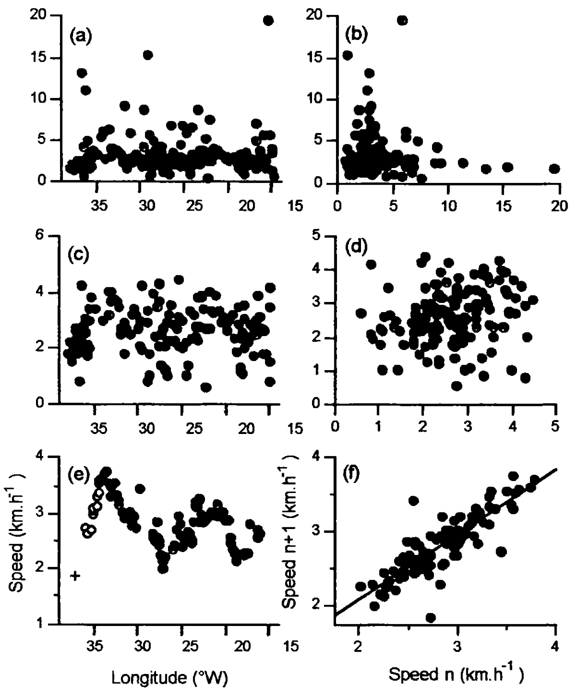

Figure 2.4. Speeds of travel during the migration from Ascension Island to Brazil and the subsequent southerly travel along the Brazilian coast and the autocorrelation between consecutive speeds. (a-b) Unfiltered data (for Fig 2.4b, $F_{1,174} = 0.5$, $p = 0.49$). (c-d) Speeds of travel > 5 km.h^{-1} removed (for Fig 2.4d, $F_{1,149} = 5.9$, $r^2 = 0.04$, $p = 0.016$). (e-f) Fully filtered data using only locations at least 90 km apart to determine speed. (for Fig 2.4f, $F_{1,110} = 283$, $r^2 = 0.74$, $p < 0.001$). For Fig. 2.4e, ● = speeds where both locations were obtained during oceanic migration, ○ = speeds where one point was during oceanic migration and the other during coastal travel, + = speeds where both points were during coastal travel.

Recommendations for future Argos tracking studies

It is intuitively obvious that the accuracy of locations will impact the calculated speed of travel in any tracking studies but while this issue has been extensively explored for conventional radio tracking (e.g. Priede 1992) it has received much less attention for satellite tracking. The fundamental advantage of the approach we have detailed here is that it rigorously defines the impacts of location accuracy in Argos satellite tracking studies and produces values for speed of travel that have known (and user specified) accuracy. We conservatively set d_{min} using the accuracy of LC B. However, our approach could be modified to take into account any difference in the accuracy class for pairs of locations (e.g. a location of class B coupled with one of class A, 1 or 2) so that the speeds of travel over smaller spatial scales could be quantified if necessary. Similarly, if animals travel in extended arcs, rather than straight lines, calculations for the distance travelled might incorporate the straightness index of segments.

For marine studies where LCs A and B often dominate, it is clearly important to know the accuracy of these locations. However this information is not provided by Argos and, consequently, little is known of the their respective accuracies (but see, for example, Britten et al. 1994 and Boyd et al. 1998). Hence it is prudent for researchers to determine the respective accuracies of LCs A and B for themselves. However, this may not be a simple procedure since the accuracy of these locations may, potentially, be dependent on the exact nature in which they are generated. For example, a class A location obtained for a migrating turtle might not necessarily have the same accuracy as a class A location obtained by a turtle on its foraging grounds due to differences in diving behaviour influencing the time separation between uplinks which in turn may effect location accuracy. However, such subtle examination of the accuracy of class A and B locations is logistically impossible in many studies and the most reasonable approach to assess their accuracy, and that used here, is simply to use trials with PTTs in fixed locations.

Our examination of Argos locations from a single turtle migrating from Ascension Island to Brazil revealed hitherto undescribed variation in the speed of travel. These variations are systematic, with the turtle travelling more slowly over certain sections of the journey and faster over others. It is important to note that this systematic variation, as shown clearly by the autocorrelation between consecutive speeds, was based on independent pairs of locations, i.e. both the locations used to calculate the first speed of travel were different to the two used to calculate the second speed of travel and so on. Hence this autocorrelation is not an artefact of our data analysis but represents a real biological signal. Similarly, once the turtle arrived at the coast of Brazil, the speed of travel decreased significantly. As such variations in speed have not been rigorously identified before, our understanding of their causality is still in its infancy. Factors that may potentially contribute to this observed variation include hydrography, i.e. the assistance to travel provided by prevailing currents; the proportion of time individuals spend actively swimming during migration rather than resting; or (for green turtles in coastal areas since these are benthic herbivores) the proportion of time they spend feeding.

In summary, the approach we have described here will allow the rigorous determination of variations in speed of travel for satellite tracked animals. As the availability of environmental data collected over large spatial scales improves (e.g. from satellite observations) and the biological parameters provided via satellite transmitters increases (e.g. dive information), so hypotheses can be developed as to the causality of variations on speed of travel during long-distance movements.

Acknowledgments

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CHAPTER III

Methods

1. Composition of the data set

In order to analyse the variables affecting the speed of travel of green turtles during migration, I used three types of data. First of all, location data, which provide information on the position of each individual at a given time. Using this location information, it was possible to calculate the speed of travel of the individuals. The speed was estimated by dividing the distance covered between two satellite locations by the time elapsed between the two locations. Secondly, the size of the turtles was measured because it is one of the factors likely to affect the speed of travel (as I mentioned for other species in the first chapter). Finally, ocean current information was collected because the performance of the individuals during migration could be affected by the oceanographic conditions they encounter whilst migrating.

During the last decade, satellite telemetry has proved to be very successful for the tracking of migrating animals. This technology has provided scientists with enough information to reconstruct the routes followed by marine animals, routes that were only suspected before (through mark-recapture studies). The mechanisms behind satellite tracking have been described in Luschi *et al.* (1996), Luschi *et al.* (1998) and Hays *et al.* (1999) among others, but in short the satellite transmitters attached to the tracked animals send binary information to a satellite of the Argos Location System during an overpass of the satellite. For marine animals, transmission only occurs when individuals are at the surface, as the transmitter is switched off whilst the individual is underwater.

Satellite transmitters were attached by Luschi, P. and Hays, G.C. (Luschi et al., 1998) to six female green turtles in 1997 and to seven others in 1998. Attachments were made at the end of their nesting season on Ascension Island (7° 57′S, 14°22′W), as it was expected that turtles would begin their migration back to Brazil shortly after attachment. Details of the attachment and processing of the obtained data have been previously explained by Luschi *et al.* (1998) and Hays *et al.* (1999) (see table 3.1 for details of each turtle and the type of transmitter attached).

Locations were obtained through the Argos system, which allocates different locations classes as a function of the accuracy of the estimated location (described in detail in chapter II). The transmitters also carry a saltwater switch, which provides a value for the mean dive duration and the number of dives for every six-hour period. This information, together with the locations, is sent every time the transmitter is at the surface if the satellite is overhead (Argos User′s manual).

Green sea turtles spend the majority of their time underwater, and their surface intervals are usually fairly short, consequently the vast majority of the locations are of a low accuracy (Hays *et al* 2001). As previously done by Luschi et al. (1998), locations of class Z (they are obtained only from one uplink) were eliminated because of their very poor accuracy. Also, locations that were obviously wrong, for example when the speed of travel was physiologically unrealistic (too rapid) for a turtle were not included for the analysis.

Table 3.1. Platform Terminal Transmitter number and model, Season of deployment and Size (Curve Carapace Length (cm)) of every turtle included in the study.

Turtle	PTT number	Transmitter model	Season of deployment	CCL (cm)
1	4650	ST-14	1998	109
2	4651	ST-14	1998	107
3	4662	ST-6	1998	105
4	11678	ST-6	1998	111
5	11680	ST-6	1998	119
6	11681	ST-6	1998	118
7	11683	ST-14	1998	113
8	6611	ST-14	1997	120
9	6614	ST-14	1997	112
10	6615	ST-14	1997	110
11	11682	ST-14	1997	117
12	11683	ST-14	1997	107

Argos provided longitude, latitude, location class, date and Greenwich Meridian Time for every location. In addition, distance, direction and speed between two locations were calculated using EXCEL, and all were computed to obtain a first worksheet for each turtle (`see table 3.2). Methods of calculation of each variable are described in Luschi et al. (1998).

Graeme Hays and Paolo Luschi measured the Curved Carapace Length of each individual after egg laying and before attachment of the transmitters.

The prevailing oceanic current that green turtles encounter during migration is the South Atlantic Equatorial Current (or SEC). The speed of the current was previously determined by Luschi *et al.* (1998) using a Global Isopycnic Model (or GIM, see also Marsh *et al.* 1998). The GIM provides information for each 1.25° of longitude and latitude of two vectorial components of the ocean current speed (north-south and east-west). Since speed values have already been reported to be fairly similar for the months of May, June and July (Hays *et al.* 1999), The values of the month of May were used when analysing the effect of the ocean current on the speed of travel of the turtles (see table 3.3 for the values of the ocean current during the month of May).

Table 3.2. Example of the worksheet built for every turtle to calculate distance, time, speed and direction of the turtle at a particular location. 'Date/time (GMT)' is the date and the Greenwich Meridian Time at which the location was obtained; 'Lat (°S)', latitude in degrees south; 'Long (°W)', longitude in degrees west; 'LC', location class; 'Dist', distance (km) between the actual location and the previous one; 'Dir (°)', direction of the turtle at that location; 'Time', the time elapsed between two locations and 'Vel (km/h)', the speed of the turtle.

Date/time (GMT)	Lat. (°S)	Long. (°W)	LC	Dist (km)	Dir (°)	Time (hrs)	Vel (km/h)
30-May 5.00	7.92	14.40					
31-May 8.25	8.21	14.85	A	59.23	237	27.42	2.16
31-May 15.43	8.94	16.73	A	222.04	249	7.31	30.39
31-May 17.45	7.84	15.07	A	220.19	57	2.03	108.39
03-Jun 4.05	7.95	14.47	0	66.39	101	58.34	1.14
03-Jun 19.57	7.87	14.43	A	10.38	25	15.85	0.65
04-Jun 14.57	7.87	14.46	A	3.22	248	19.01	0.17
05-Jun 6.31	7.45	13.54	A	111.93	65	15.56	7.19
05-Jun 14.48	7.85	14.44	A	108.70	246	8.29	13.12
07-Jun 3.21	7.97	14.28	A	22.84	127	36.55	0.62
07-Jun 7.34	7.91	14.43	A	17.63	291	4.22	4.18
08-Jun 19.46	7.88	14.44	A	3.50	342	36.20	0.10
09-Jun 6.47	7.92	14.43	3	3.95	169	11.02	0.36
10-Jun 8.06	7.91	14.42	A	0.86	50	25.31	0.03
10-Jun 15.33	7.93	14.37	A	6.29	101	7.44	0.85
11-Jun 18.36	7.91	14.45	A	9.43	281	27.06	0.35
12-Jun 2.26	7.93	14.38	A	7.83	104	7.84	1.00

Table 3.3. Ocean current information for the month of May

Lat(°S)	Long (°W)	Dir(°)	Speed (km/h)	North-south	East-west
5.625	14.375	241	0.62	-8.43	-15.04
6.875	14.375	245	0.52	-6.07	-12.97
8.125	14.375	248	0.45	-4.65	-11.63
9.375	14.375	247	0.36	-3.92	-9.18
5.625	15.625	246	0.6	-6.85	-15.19
6.875	15.625	251	0.5	-4.62	-13.12
8.125	15.625	252	0.43	-3.68	-11.46
9.375	15.625	247	0.34	-3.59	-8.63
5.625	16.875	250	0.59	-5.53	-15.34
6.875	16.875	254	0.49	-3.78	-12.99
8.125	16.875	253	0.41	-3.28	-10.78
9.375	16.875	245	0.31	-3.56	-7.73
5.625	18.125	251	0.58	-5.17	-15.34
6.875	18.125	254	0.48	-3.77	-12.76
8.125	18.125	252	0.38	-3.33	-10.06
9.375	18.125	243	0.28	-3.5	-6.97
5.625	19.375	251	0.58	-5.24	-15.19
6.875	19.375	253	0.48	-3.98	-12.63
8.125	19.375	251	0.37	-3.34	-9.61
9.375	19.375	243	0.26	-3.24	-6.48
5.625	20.625	250	0.58	-5.42	-15.15
6.875	20.625	252	0.48	-4.08	-12.74
8.125	20.625	251	0.36	-3.21	-9.46
9.375	20.625	246	0.24	-2.8	-6.2
5.625	21.875	250	0.58	-5.5	-15.23
6.875	21.875	252	0.49	-4.22	-12.99
8.125	21.875	251	0.36	-3.33	-9.5
9.375	21.875	245	0.24	-2.83	-6.05
5.625	23.125	250	0.58	-5.53	-15.1
6.875	23.125	251	0.5	-4.55	-13.12
8.125	23.125	248	0.37	-3.9	-9.61

Table 3.3. Continued.

Lat(°S)	Long (°W)	Dir(°)	Speed (km/h)	North-south	East-west
9.375	23.125	239	0.25	-3.59	-5.86
5.625	24.375	249	0.57	-5.6	-14.78
6.875	24.375	249	0.5	-4.97	-12.97
8.125	24.375	245	0.38	-4.52	-9.52
9.375	24.375	232	0.25	-4.37	-5.5
5.625	25.625	250	0.55	-5.26	-14.29
6.875	25.625	249	0.49	-4.84	-12.72
8.125	25.625	244	0.38	-4.52	-9.39
9.375	25.625	230	0.25	-4.49	-5.33
5.625	26.875	253	0.51	-4.11	-13.63
6.875	26.875	252	0.46	-3.9	-12.27
8.125	26.875	247	0.35	-3.89	-9.03
9.375	26.875	231	0.23	-4.07	-5.03
5.625	28.125	258	0.47	-2.64	-12.74
6.875	28.125	257	0.42	-2.67	-11.4
8.125	28.125	249	0.32	-3.13	-8.27
9.375	28.125	232	0.21	-3.6	-4.62
5.625	29.375	267	0.43	-0.65	-11.99
6.875	29.375	264	0.37	-1.07	-10.33
8.125	29.375	254	0.27	-1.99	-7.16
9.375	29.375	238	0.18	-2.64	-4.24
5.625	30.625	286	0.43	3.38	-11.48
6.875	30.625	281	0.35	1.88	-9.42
8.125	30.625	277	0.23	0.75	-6.26
9.375	30.625	277	0.14	0.48	-3.98
5.625	31.875	318	0.54	11.11	-10.06
6.875	31.875	313	0.4	7.6	-8.22
8.125	31.875	312	0.31	5.7	-6.37
9.375	31.875	315	0.25	4.95	-4.88
5.625	33.125	340	0.58	15.19	-5.45
6.875	33.125	335	0.41	10.45	-4.82

2. Data transformation

A worksheet was compiled for the analysis using EXCEL and MINITAB as software. This worksheet included all the possible variables, which could influence the travelling speed of the turtles during migration. A total of eleven variables were selected for the analysis: (1) the overall speed of the ocean current, (2) the north-south and (3) east-west components of the ocean current velocity, (4) the size of the turtle (CCL), (5) the mean dive duration, (6) the standard deviation of the mean dive duration, (7) the number of dives, (8) the straightness index (see below for its calculation), (9) the direction of the ocean current, (10) the turtle direction, and (11) the angle between these two directions (see table 3.4). In order to evaluate the influence of these selected variables on the travelling speed of the tracked turtles, the migration routes were divided in cells of 1.25° of longitude and latitude (see migration routes at figure 3.1), since the ocean current information was in that format. A value for each of the eleven variables was calculated for each cell. Values of each variable were obtained for a total of 47 cells.

a) Data transformation of the ocean current

The original values of the speed of the ocean current were given as vectors. For the analysis, we transformed the values into km/h. In addition, the direction of the current for each cell was calculated.

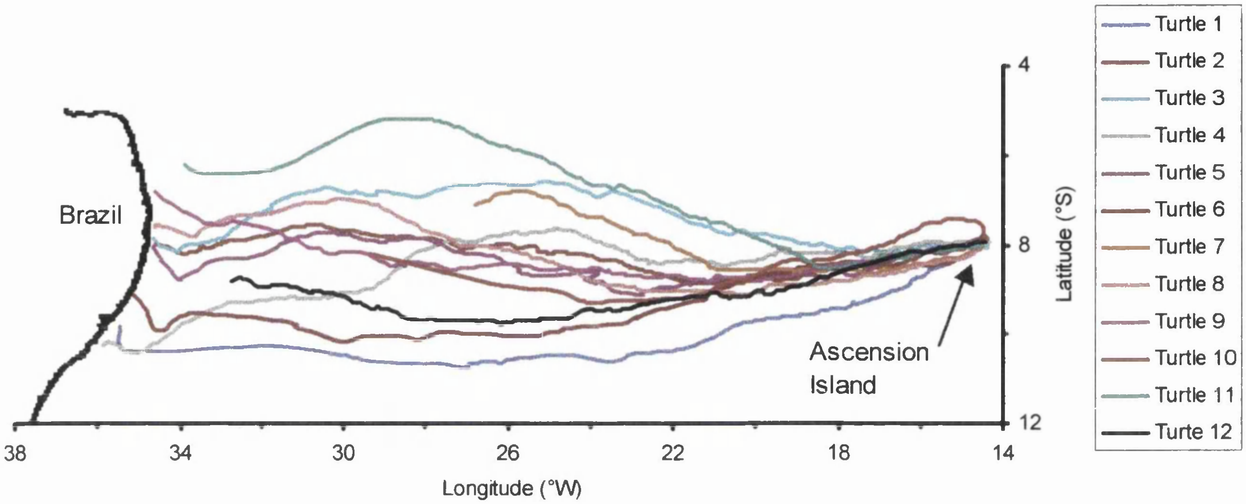

Figure 3.1. Routes of migration of the 12 turtles studied from the nesting grounds at Ascension Island (7° 57' S, 14° 22' W) to the feeding grounds at the coast of Brazil (between 5°-10° S and approximately 35° W)

Table 3.4. Variables included in the analysis: 'PTT' (PTT number), 'CCL' (cm), 'Long' (longitude (°W) of the second location of a cell), 'Lat' (latitude (°S) of the second location of a cell), 'Tspeed' (the speed of the turtle (km/h)), 'Tdir' (turtle direction), 'Str In' (straightness index), 'Cdir' (current direction), 'Csp' (speed of the current (km/h)), 'east-we' and 'north-so' (east-west and north-south components of the speed of the current), 'angle' (angle between the directions of the turtle and of the current), 'MDD' (Mean Dive Duration (min)), 'N' (number of dives) and 'SD' (Standard Deviation of the Mean Dive Duration).

Turtle	PTT	CCL	Lat	Long	Lat	Tspeed	Tdir	Str. In	Cdir	Csp	North-so	East-we	Angle	MDD	N	SD
1	4650	109	8,125	15,625	8,125	2.78	245	97	252	0.43	-3.68	-11.46	6.99	6.57	4	1.38
1	4650	109	8,125	16,875	8,125	2.35	256	96	245	0.31	-3.56	-7.73	11.18	5.91	6	2.26
1	4650	109	9,375	18,125	9,375	2.44	261	99	243	0.28	-3.5	-6.97	18.17	6.25	8	1.98
1	4650	109	9,375	19,375	9,375	2.89	258	99	243	0.26	-3.24	-6.48	14.55	6.42	7	2.37
1	4650	109	9,375	20,625	9,375	3.33	248	99	246	0.24	-2.8	-6.2	1.60	5.26	3	0.62
1	4650	109	9,375	21,875	9,375	3.02	265	99	245	0.24	-2.83	-6.05	20.23	6.59	6	2.74
1	4650	109	9,375	23,125	9,375	2.76	273	99	239	0.25	-3.59	-5.86	33.72	7.86	5	2.46
1	4650	109	9,375	24,375	9,375	2.60	267	100	232	0.25	-4.37	-5.5	35.49	6.91	7	2.34
1	4650	109	9,375	25,625	9,375	2.48	264	96	230	0.25	-4.49	-5.33	34.36	8.20	6	2.4
1	4650	109	9,375	26,875	9,375	2.12	273	99	231	0.23	-4.07	-5.03	42.06	8.49	6	2.14
1	4650	109	9,375	29,375	9,375	2.42	281	98	238	0.18	-2.64	-4.24	43.20	9.45	9	3.33
2	4651	107	6,875	14,375	6,875	2.68	259	85	248	0.45	-4.65	-11.63	11.27	3.27	8	0.73

b) Straightness index

The straightness index gives an indication of how straight the route followed by a turtle within a given cell is. If the straightness index is low, the speed of travel is likely to be overestimated, as the distance actually covered by the individual between two satellite locations is greater than the calculated one. The straightness index of a cell is calculated by adding distances between consecutive locations, and then dividing the result by the straight distance between the first and last locations of the cell. This ratio is then multiplied by 100 to obtain a percentage. Only the cells with a straightness index greater than 96% were kept for analysis. This threshold was established using a stepwise multiple regression: 96% was the level at which the influence of the straightness index on the speed of travel was not significant ($p \geq 0.05$).

c) Travelling speed and direction followed by the tracked individual

In order to estimate the speed of travel of an individual within a given cell, a minimum distance of 90 km between two locations was decided to be necessary for the speed estimations to be of acceptable accuracy (see chapter II). From all the speed estimations obtained for a given cell, we calculated their mean value in order to allocate a single speed value for each cell.

In every cell, the two locations the most apart from each other were selected, with a minimum distance between them of 103.545 km, which represents 75% of 1.250° (195.23

km is the maximum distance of the cell). If this requirement was not met, the first location within the next cell was used as second location in the calculation, with the condition of not being more than 10% of the total distance of the next cell. Once the two locations were selected for every cell, the direction the individual was heading to in this cell was calculated.

d) Angle between the direction of travel and the direction of the ocean current

This angle represents the angle formed between the directions of movement of the turtle and the direction of the ocean current. It is calculated as the difference between the two directions. If the angle is small, the turtle is likely to be taking advantage of swimming with the current. On the other hand, wider angles mean that the turtle is likely to be facing the current as an obstacle during the migration.

e) Mean dive duration, standard deviation and number of dives

A value of the mean dive duration over a 6-hour period is recorded by the transmitter and sent to the satellite when it is passing overhead. First, two locations situated the furthest apart from each other within a given cell were selected. Then, I calculated the mean of all the mean dive duration values in that cell, the corresponding standard deviation, and the mean number of dives. This way, a mean dive duration, a standard deviation and a number of dives are allocated to each cell.

f) Speed and direction through the water

In addition to the calculation of the speed of travel related to the ground, we estimated the speed and direction of the turtle through the water. This was obtained by simple vector subtraction of the vector of velocity of the current from the vector of ground velocity. The results will provide information of the swimming effort of the turtles according to the variation of speed and direction of the current. A value of speed of the turtles through the water was obtained for each cell. The results were compared to their ground speed and to the current speed.

3. Comparison against the speed of travel and mean dive duration for a Malaysian population of green sea turtles

The results obtained from the Ascension Island turtles were compared to the results obtained from another population of migrating sea turtles (five individuals) from the South China Sea. Dr. Paolo Luschi let us use the Argos location information and dive duration to compare the overall performance of five Malaysian green turtles during migration, to that of Ascension Island turtles. This information had been previously collected as a part of a research program on the biology and migration of West Malaysian green turtles (see Luschi *et al.* 1996 and Papi *et al.* 1995). The nesting grounds of this population are located at Pulau Redang Island (5° 49′N, 103° 00′E), and the feeding grounds at different locations, i.e. Borneo, Bugsuk Island and Bangka (see Luschi et al. 1996). Only values of mean speed and mean dive duration during migration were calculated (table 3.5). No information of ocean currents or body size of the turtles was available.

A relationship was found between diving behaviour and speed of travel at the analysis of data of Ascension Island population (explained in chapter iv). The aim of the short study was not to carry out a detail analysis of the factors affecting the speed of travel during migration of the Malaysian population but to test similar relationships between speed of travel and diving behaviour in other populations of sea turtles.

Table 3.5. Mean Dive Duration (min) 'MDD' and Mean Speed of Travel (km/h) 'Speed' of two populations of green sea turtles: Ascension Island population (Asc) and Malaysia population (Mal) during their respective migrations.

Turtle	Population	MDD	Speed
1	Asc	7.09	2.57
2	Asc	5.10	2.44
3	Asc	10.70	2.22
4	Asc	3.41	2.72
5	Asc	3.78	2.32
6	Asc	2.93	2.46
7	Asc	3.24	2.79
8	Asc	5.00	2.86
9	Asc	6.84	2.47
10	Asc	5.21	2.15
11	Asc	5.61	2.54
12	Asc	10.99	1.81
13	Mal	2.54	2.29
14	Mal	4.62	1.87
15	Mal	3.18	1.55
16	Mal	5.92	1.38
17	Mal	3.79	2.22

CHAPTER IV

Results

To achieve a better understanding of the different factors which could possibly influence the speed of travel, two types of analysis were considered: a detailed analysis made by dividing the whole migration route into pixels of 1.25° longitude x 1.25° latitude (n = 47 cells) and a general study on the overall speed of travel during migration.

Detailed analysis of speed of travel during migration

The average mean speed of turtles migrating from Ascension Island to Brazil was 2.59 km/h (range: 1.90-3.02 km/h, n=12) (see table 4.1 for mean, maximum and minimum speeds of each turtle during migration).

Mean dive duration, number of dives performed, as well as the angle between the direction of the turtle and that of the current, all significantly influenced the speed of travel of the turtles. (Stepwise Multiple Regression: R^2=51.79, $p<0.05$). These three factors together explain 51.79% of the variation in speed; 48.19% was explained by the overall diving behaviour (duration and number of dives), and 36.59% by the mean dive duration alone. Fewer dives and dives of a shorter duration appeared to lead to a faster speed of travel. In addition, speed was greater when the direction of travel of the animal was close to that of the ocean current.

Table 4.1. Minimum speed of travel (km/h), location at which the speed is minimal (°W, °S), maximum speed of travel (km/h), location at which the speed is maximal (°W, °S), mean speed of travel (km/h) and size of the turtle (cm).

Turtle	Min Speed	Location of min Speed (° S, ° W)	Max Speed	Location of max Speed (° S, ° W)	Mean Speed	Size
1	2.12	10.63, 27.902	3.34	10.354, 21.797	2.66	109
2	1.94	8.189, 33.947	4.14	8.907, 21.829	2.64	107
3	1.60	7.892, 33.108	3.40	7.841, 20.743	2.22	105
4	1.44	10.270, 35.885	4.07	8.368, 21.730	2.72	111
5	0.96	8.179, 15.424	3.47	8.361, 16.823	2.51	119
6	1.09	8.441, 15.125	4.29	10.190, 29.560	3.02	118
7	2.33	8.255, 21.530	3.88	8.326, 15.600	2.89	113
8	2.11	7.559, 34.501	3.33	8.400, 15.666	2.88	120
9	1.51	8.004, 15.222	3.24	8.451, 18.161	2.45	112
10	1.98	7.392, 15.259	3.27	7.805, 16.464	2.59	110
11	1.83	5.892, 25.709	3.42	8.152, 15.649	2.64	117
12	1.28	9.706, 26.717	3.43	8.259,16.548	1.90	107

a) Diving behaviour

The speed of travel of a turtle was negatively correlated with mean dive duration, standard deviation of the mean dive duration and number of dives performed. Short dives of fairly constant duration (small standard deviation), and a smaller number of dives performed, resulted in an increased overall speed of travel.

b) Ocean current

There was also a negative correlation between the speed of the turtle and the angle between the direction the individual was heading and that of the ocean current (the wider the angle, the slower the speed). Hence, the ocean current can potentially have a positive effect on the speed of the turtle if the animal is travelling in the same direction that the current.

c) Body size

The body size of the turtles also affected performance. There was a positive correlation between size and speed of travel, suggesting that larger turtles swim faster than smaller turtles. In addition, there was a negative correlation between (1) size and mean dive duration, with larger animals performing shorter dives as indicated by shorter mean dive durations, (2) between size and number of dives performed by an individual, with larger animals performing less dives, and (3) between the size and the standard deviation of the mean dive duration, with larger turtles showing a more consistent behaviour during migration than smaller ones.

The effect of the size of the turtles on their diving behaviour, together with the relationshipbetween diving behaviour and speed of travel, suggest that the speed of travel will be determined by the duration of dives, the corresponding standard deviation of the mean dive duration, and the number of dives, factors which are dependent on the size of the animal.

d) Maximum and minimum speeds

In general maximum speeds during migration were concentrated in the first half of the migration trip, are rarely present in the second part of the migration route (only one individual reached its maximum speed during the second part) (Fig. 4.1). Seven turtles reached their maximum speed at the very beginning (between 15° and 19° of longitude west) and four others between 20° and 22° of longitude west. The locations of the minimum speeds of travel were more variable, with four turtles reaching their minimum speeds just after leaving Ascension Island, four others before arriving to Brazil, and three at the middle of their route, between 25° and 28° of longitude west (Fig. 4.1).

Some turtles increased their speed of travel at the very beginning of the migration (for instance, turtles 5, 6 and 9, Fig. 4.2-e,f,i) and/or decreased the velocity at the very end, just before arriving to Brazil (for example, turtles 2, 4, 5 and 8) (Fig. 4.2-b,d,e,h). In some cases, it is possible that the actual speed at the start of migration was higher than the estimated. Indeed, the transmitters could have sent locations before the turtle did actually leave the island and started the migration, and the time between two locations would therefore be overestimated and the speed underestimated (see Fig. 4.4a-b). Equally, the same problem could affect the estimation of the speed of the turtles at the end of the migration: turtles could have arrived to the feeding grounds and finished their travel before transmitting a location to the satellite. Thus, the speed would be overestimated because the last location would be later in time than the arrival time (see Fig. 4.4d-e).

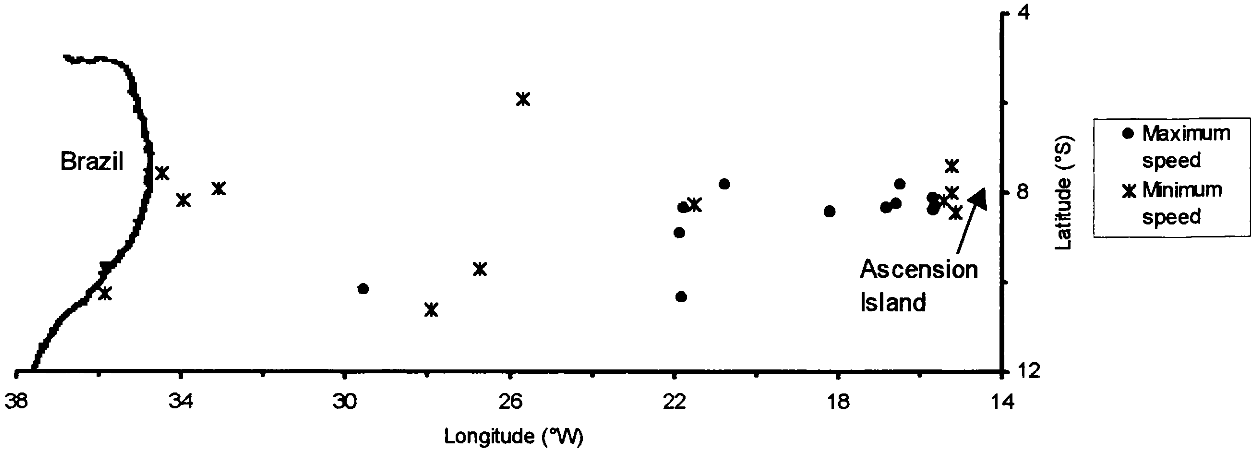

Figure 4.1. Locations at which the speed of travel is maximum and minimum for each of the 12 turtles

e) Variation in the speed of travel and the duration of dives during migration

Occasionally we observed locations at which the speed was faster or slower compared to that estimated for the previous and/or posterior set of two locations. Because these locations were selected with a minimum of 90 km between them and were consistent with the route followed, it is likely that these faster or slower speed were not erroneous and that the turtles were in fact, swimming at these speeds (see for example turtle 2 at Fig. 4.4c)

The behaviour of some of the turtles remained fairly consistent during migration, with little variation in the mean dive duration and speed of travel. Five turtles (turtles 4, 5, 6, 7 and 8, four of them are the fastest of the twelve individuals) present mean dive durations shorter than 10 min (Fig. 4.3-d,e,f,g,h), and three others (turtles 1, 2 and 11) present mean dive durations that are shorter than 20 min (Fig. 4.3-a,b,k). Overall, for these eight turtles the variation of the speed of travel was small and close to the mean value over the migration, probably as a result of the little variation of the mean dive duration (not considering the first and last few locations) (Fig. 4.2). However, there are some exceptions. For instance, turtle 1 decreased the speed around day 10 (Fig. 4.2-a), and turtle 7 (Fig. 4.2-g) around day 15, with no apparent variation of the mean dive duration at that time for either of them. It is possible that these turtles performed long dives within a six hours period, and the information was lost due to data compression (see examples A and B showing the effects of data compression in table 4.2 and Fig. 4.5). Turtle 11, slowed the speed slightly along the migration route (Fig. 4.2-k). This turtle started migrating with mean dives shorter than 10 min and increased the length of dives slightly (always under 20 min long) at the end of the migration (Fig. 4.3-k), and this explains the variation of the speed.

Among the other four turtles performing mean duration of dives longer than 20 min, two types of behaviour were observed. Turtles 9 and 10 perform long dives only at certain parts of the migration, while turtles 3 and 12 alternate long and short mean dive durations for most of the migration. The behaviour of turtle 9 was very interesting because, she only performed long mean dive durations between days 20 and 30, and mean dive durations were shorter and more constant during the rest of the trip (Fig. 4.3-i). Accordingly, the speed of travel was minimum between days 20 and 30 (with the exception of the first location which had a very low speed) (Fig. 4.2-i). The case of turtle 9 provided a very clear example of the relationship between changes in mean dive duration and changes in travel speed. Turtle 10 dived longer on average at the end of the migration with some duration means being longer than 20 min. (Fig. 4.3-j). The speed of travel of this turtle progressively decreases along migration, although speed information could not be obtained for the last part of the migration because it did not fullfil the conditions of the analysis (Fig. 4.2-j).

Only two of the twelve turtles performed mean dive durations of extraordinarily long duration: turtles 3 and 12 (Fig. 4.3-c and 4.3-l). These two small turtles (105 and 107 cm respectively) also travelled at the slowest mean speed of the twelve individuals (table 4.1 at page 52). The speed of turtle 3 did not vary largely during migration, staying slow and around its mean for most of the migration (mean = 2.22 km/h) (Fig 4.2-c). Mean dives were occasionally over 40 min long (Fig. 4.3-c). Turtle 12 was the individual performing the longest mean dive durations, with values over 60 min long (Fig. 4.3-l), its speed of the travel decreased along migration, with most values being under its mean speed (mean = 1.90 km/h) after day 25 (Fig. 4.2-l).

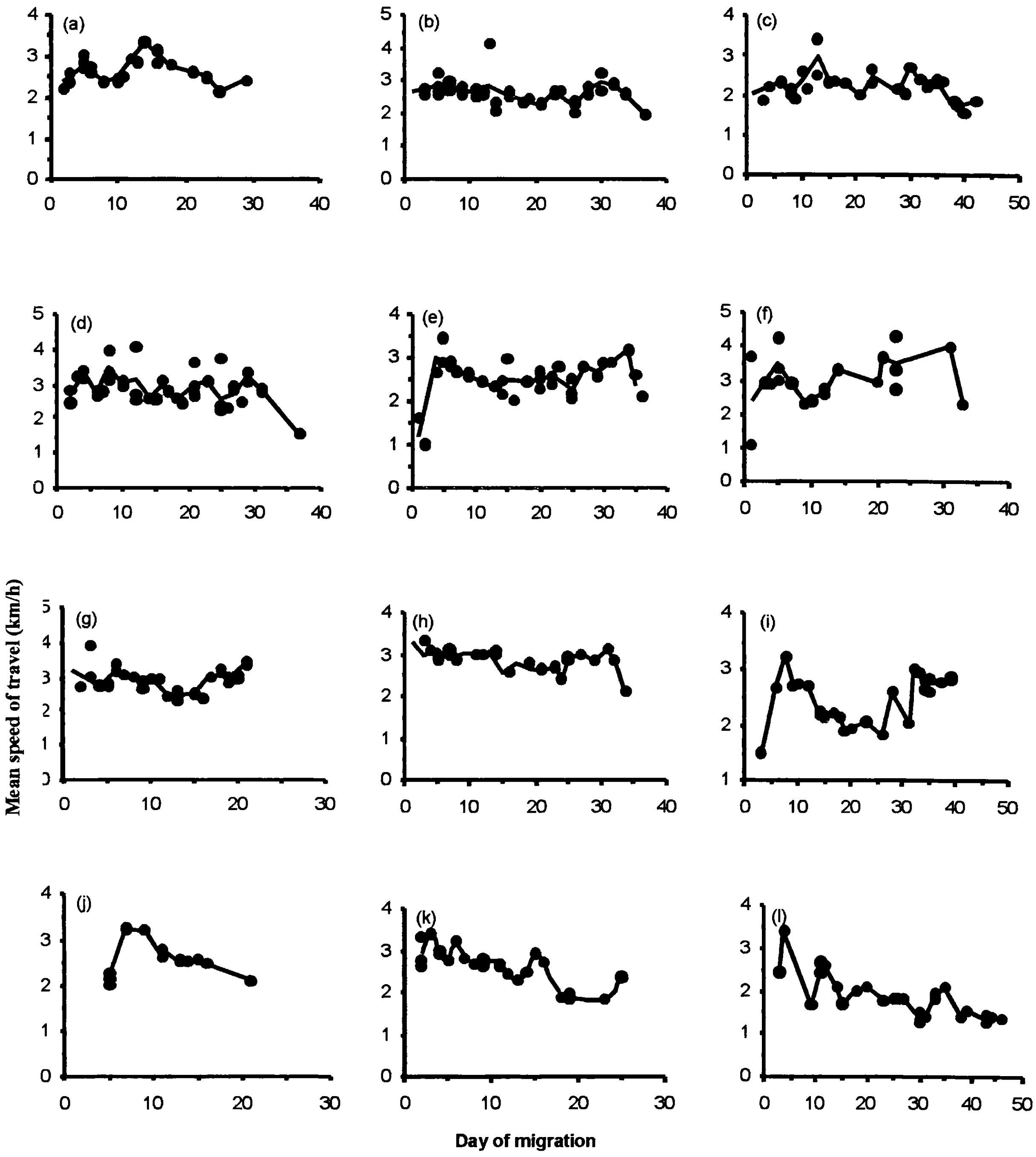

Figure 4.2.a-l. Speed of travel (km/h) of 12 female green turtles per day of migration. Graphs a. to l. are for turtles 1 to 12 respectively.

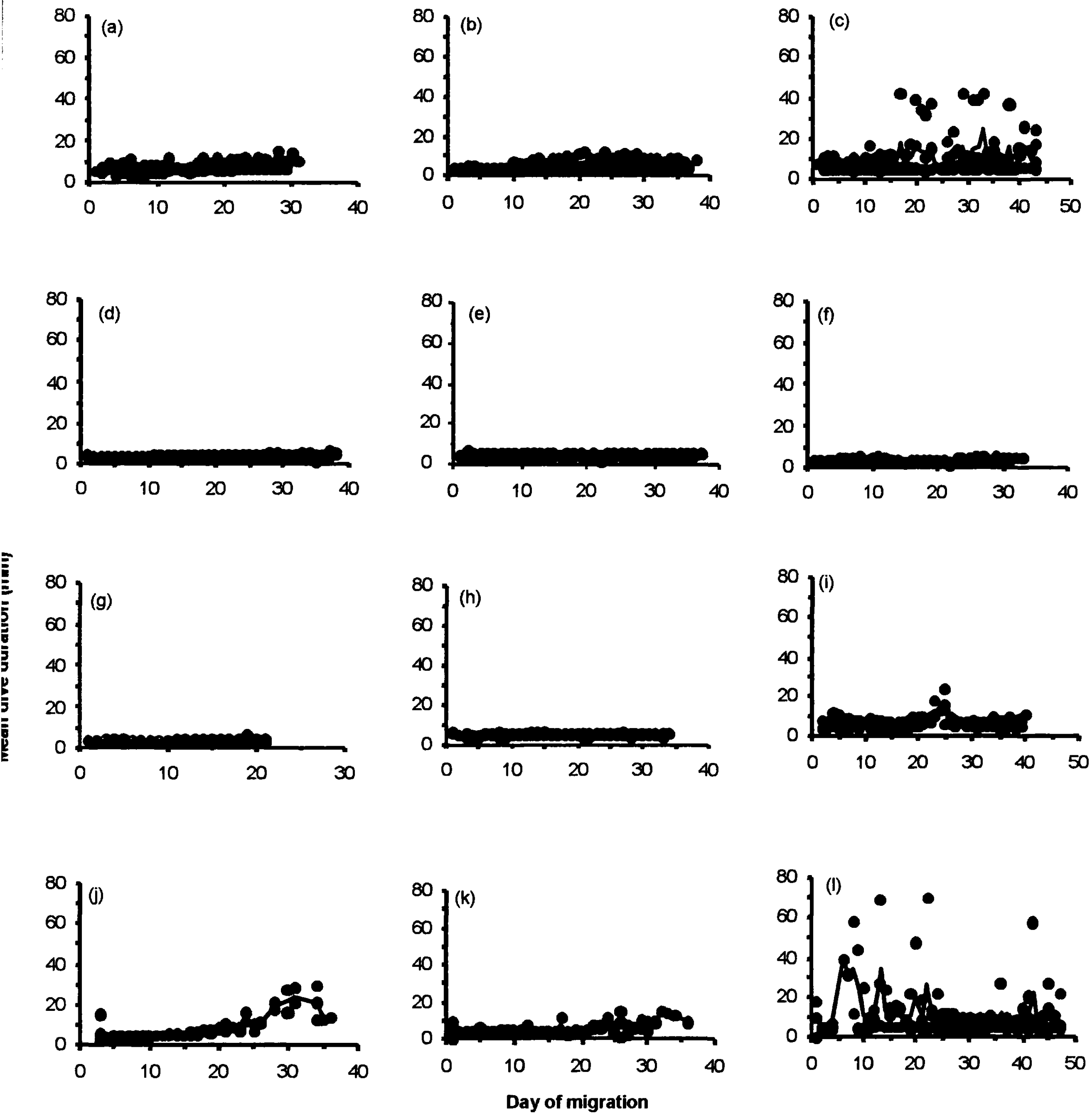

Figure 4.3. a-l. Mean dive duration (min) of 12 female green turtles per day of migration. Graphs a. to l. are for turtles 1 to 12 respectively.

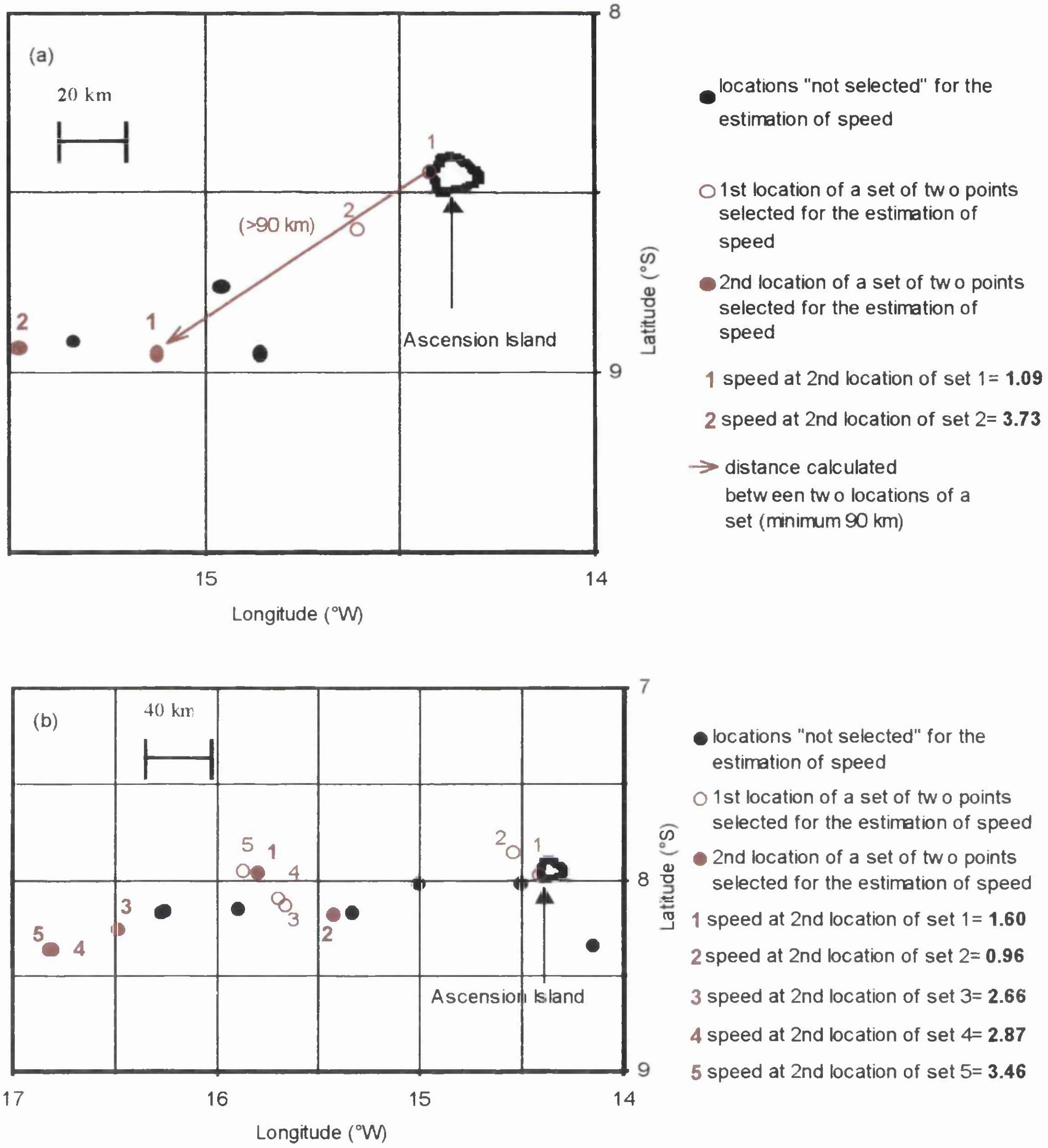

Figure 4.4a-e. Maps at specific locations during migration. Sets of two points selected for the calculation of speed are shown (same numbers correspond to the same set of two locations), as well as values of speed at the second location of each set. a) Turtle 6: beginning of migration, showing a high variation of the speed between the first two consecutive sets. b) Turtle 5: beginning of migration, shows a fast increase of the speed between consecutive sets.

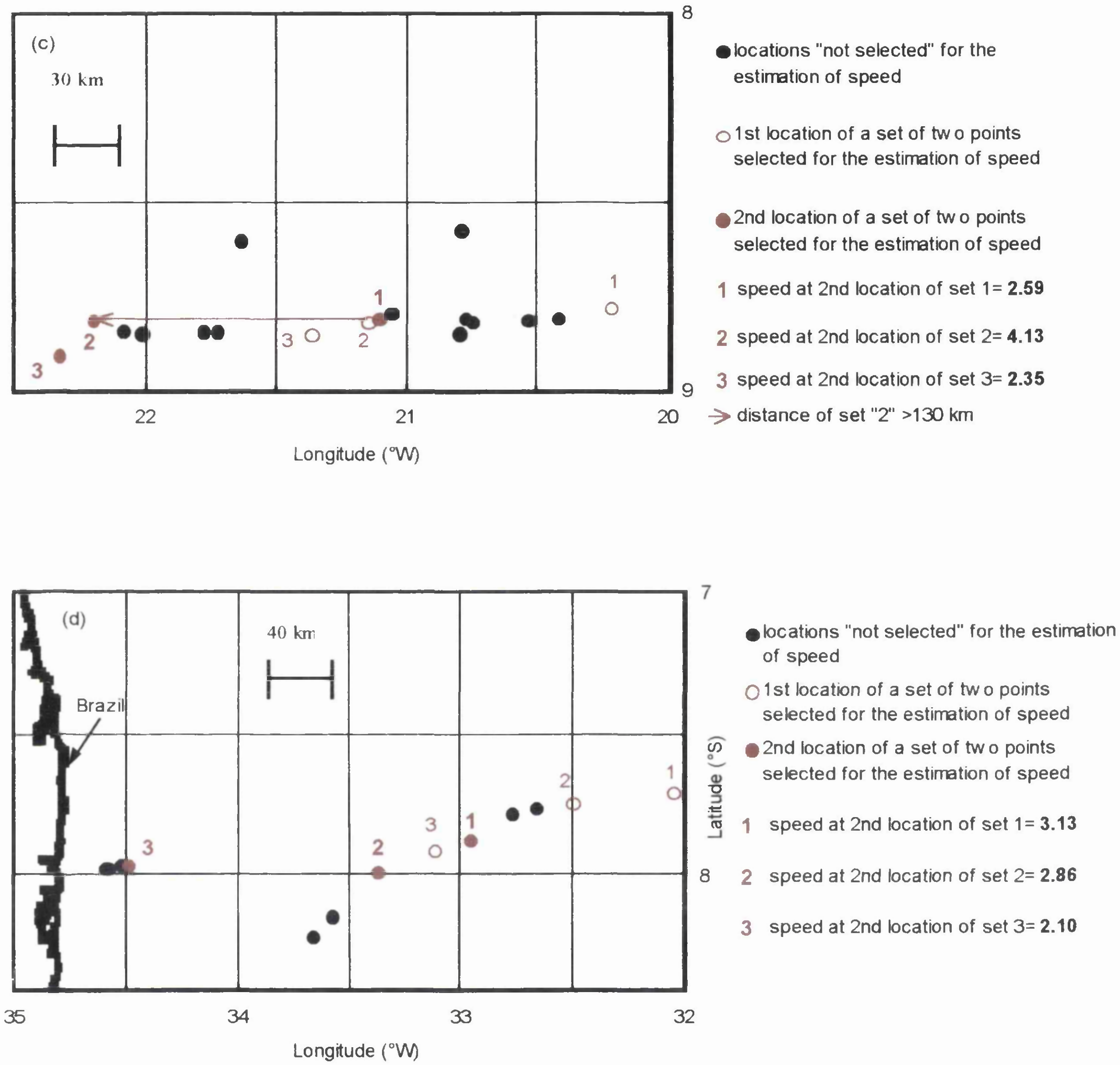

Figure 4.4. Continued. c) Turtle 2: at the middle of migration, showing locations of consecutive sets for which the speed is highly variable. d) Turtle 8: at the end of migration, showing a progressive decrease of the speed arriving to Brazil.

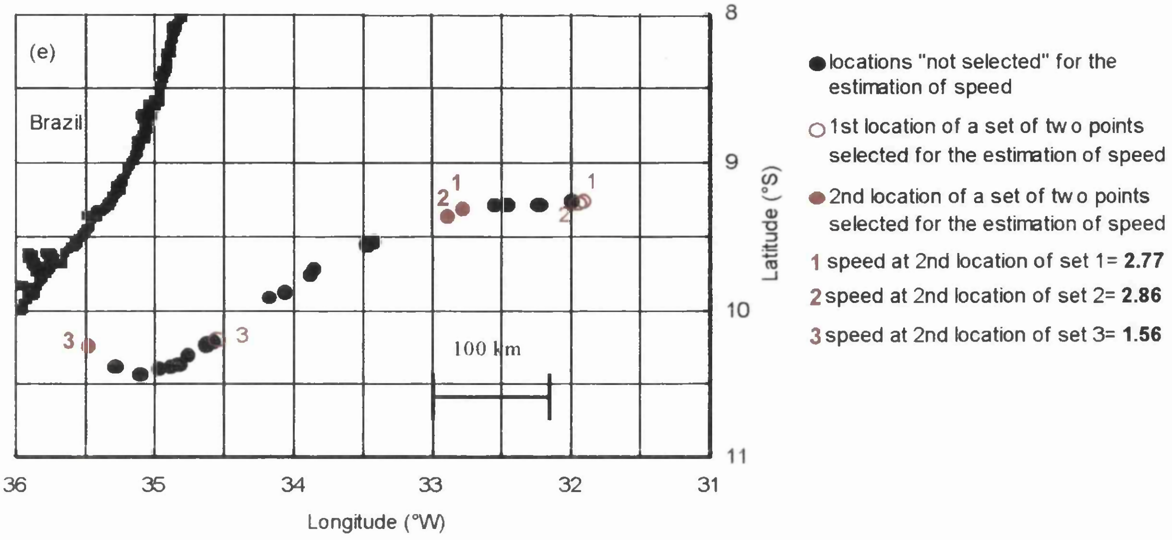

Figure 4.4. Continued. e) Turtle 4: at the end of migration, progressive decrease of the speed.

Table 4.2. Two examples (A and B), with similar mean dive duration, of the possible lost of data by compression in a six hours period. Duration of dives, number of dives of that duration, total duration, percentage of time spent performing those dives, and mean dive duration (min) for the six hour period. Example A: no data would be lost by compression. Example B: dives of long duration would be lost by data compression.

Example A				**Example B**			
Number of dives	Duration (min)	Total duration (min)	% of time	Number of dives	Duration (min)	Total duration (min)	% of time
20	5	100	28%	2	35	70	19%
15	4	60	17%	35	4	140	39%
20	6	120	33%	12	5	60	17%
10	8	80	22%	20	4.5	90	25%
Mean duration (min)	**5.54**				**5.28**		

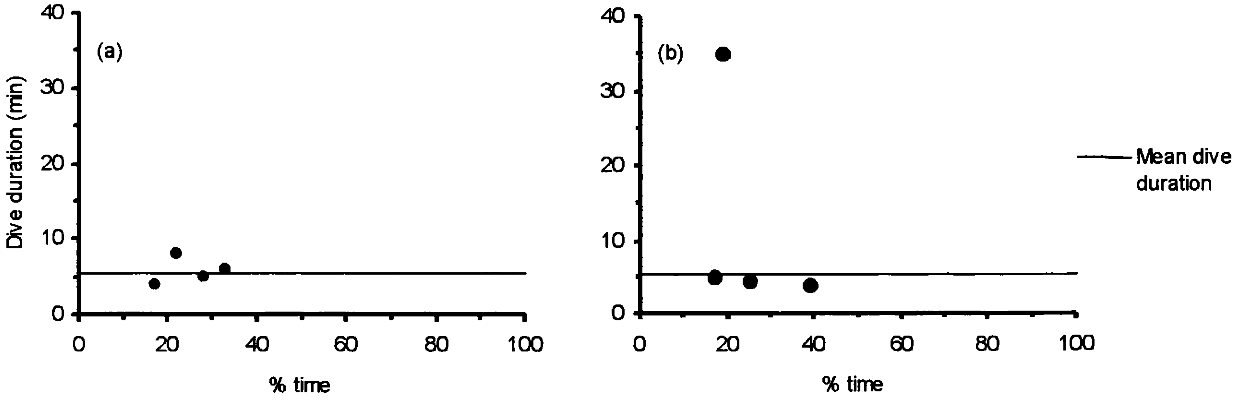

Figure 4.5. a) Example A: no data would be lost by compression, dives within a six hour period are of duration close to the mean dive duration. b) Example B: dives of 35 min would be lost.

f) Speed and direction through the water

There is not a variation of the swimming activity of the turtles as a consequence of the variation of the current speed. At high current speeds the turtle does not reduce its velocity to take advantage of the current but keeps swimming actively at the same rate (figures 4.6a-b). We can see at figure 4.6-b that there is a strong relationship between the speed of the turtle through the water and the ground speed. Thus, the ground speed of the turtle is a consequence of the variation of speed through the water and not of the current speed. The turtle keeps swimming actively independently of the variation of the current speed.

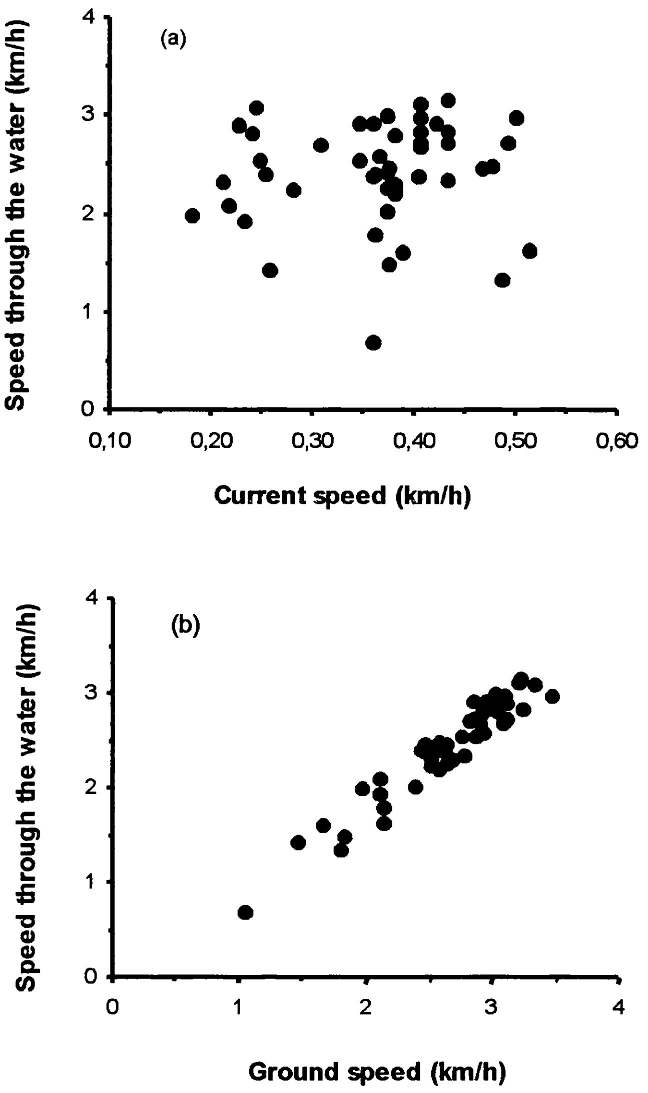

Figura 4.6. a) Speed of the turtles through the water (km/h) versus speed of the current (km/h). b) Speed of the turtles through the water (km/h) versus ground speed (km/h).

General study of speed of travel during migration

a) Dive duration

The overall speed of travel is significantly slower for turtles spending more time performing long dives (dives greater than 10 and 15 min) (Linear Regression: $p<0.05$; $R^2=0.63$ for dives longer than 10 min and $R^2=0.55$ for dives longer than 15 min) (see Fig. 4.7a-b). Long mean dive durations result in a reduction of the speed of the turtle.

b) Malaysian population of green turtles

There are significant differences between the mean speed of travel during migration for Ascension Island and Malaysia populations (T-test: $T=2.99$, $p=0.032$, $DF=5$), with a tendency for Ascension Island turtles to swim faster (Fig. 4.8-a). Although Ascension Island turtles also have longer mean dive durations during migration than turtles from Malaysia, the difference is not significant (T-test: $T=1.86$, $p=0.084$, $DF=14$, Fig. 4.8-b). Similarly to the findings for Ascension Island population, the smallest is the overall mean dive duration for Malaysia population turtles, the highest the mean swimming speed, although this relationship was not found significant in the analysis ($p=0.24$, $R^2=42\%$, $n=5$) (Fig. 4.9).

c) Body size

Finally, the size of the turtle significantly influenced the amount of time spent performing long dives (dives greater than 10 min) (Linear Regression: $p<0.05$; $R^2=0.55$). The size of the turtle explains 55 % of the variation in the percentage of time associated with these long dives. The negative relationship between size and time involved in long dives suggests that bigger turtles tend to spend a smaller proportion of their time performing long dives (Fig. 4.7c-d). Equally, the percentage of time spent performing long dives is greater in smaller turtles. The size of the animal appears to be a fundamental factor driving the diving behaviour of individuals, with smaller turtles performing on average longer dives than bigger animals. This difference in the mean length of the dives results in a variation of the overall speed of travel during migration.

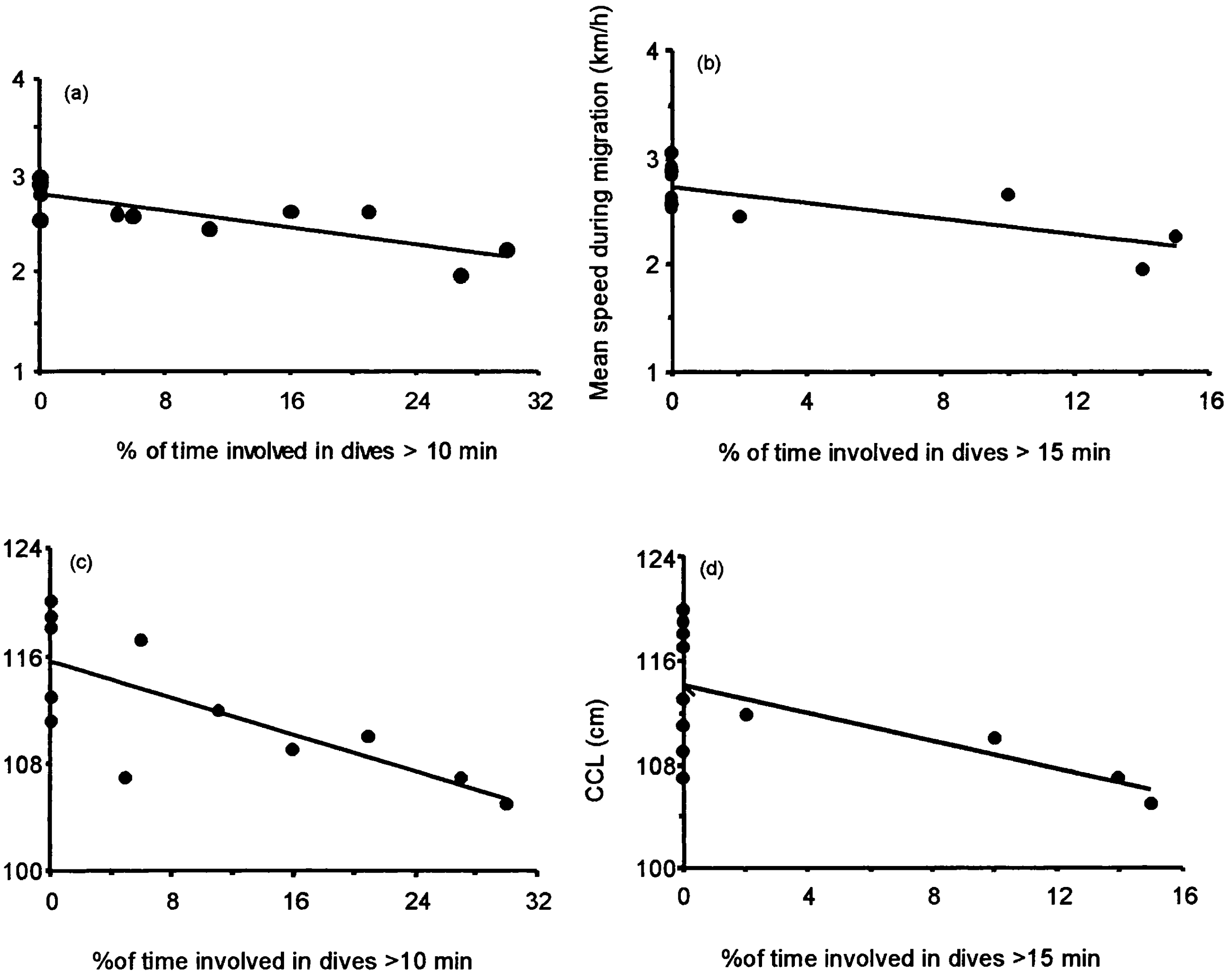

Figure 4.7.a-d. a) Mean speed during migration (km/h) versus time involved in dives longer than 10 min. b) Mean speed during migration (km/h) versus time involved in dives longer than 15 min. c) Size of the turtles (CCL (cm)) versus time involved in dives longer than 10 min. d) Size of the turtles (CCL (cm)) versus time involved in dives longer than 15 min.

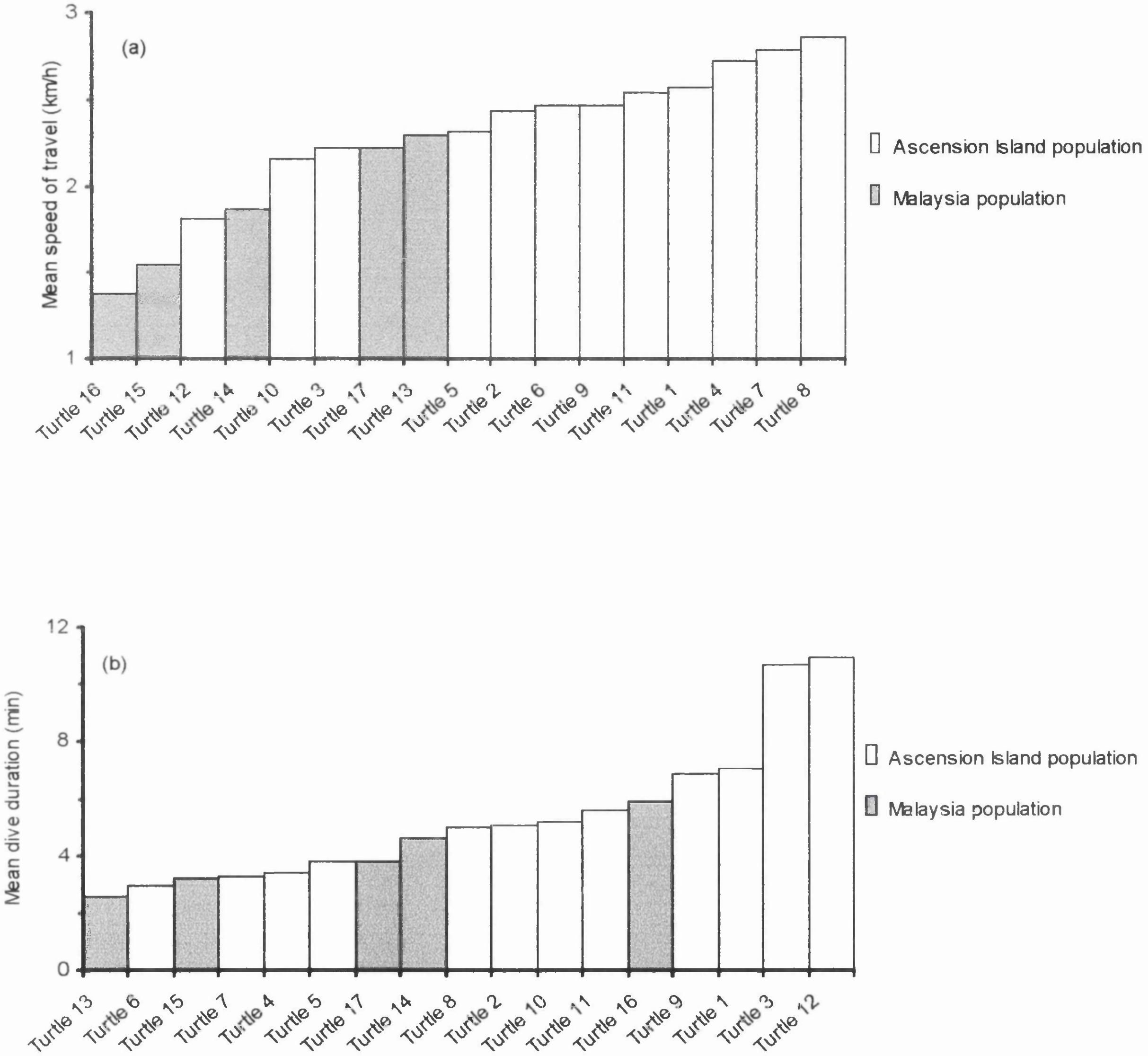

Figure 4.8. a) Mean speed of travel (km/h) of two populations of green sea turtles. b) Mean dive duration (min) of two populations of green sea turtles.

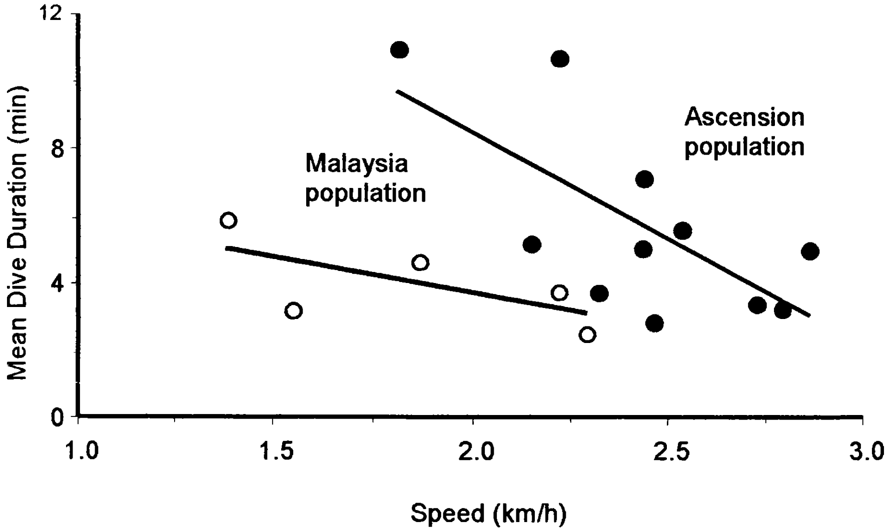

Figure 4.9. Mean dive duration (min) versus Mean speed of travel (km/h) for the two populations of green sea turtles studied.

CHAPTER V

Discussion

Implications of fasting during long distance migration

In order to understand the observed behaviour of Ascension Island migrating turtles we must consider again the special conditions in which the population of green sea turtles from Ascension Island have evolved. Ascension Island turtles are believed to feed at the Brazilian coast primarily on macroalgae, a source of food that they can find neither during their transoceanic migration, nor at Ascension Island. Thus, they are thought to survive exclusively on fat reserves during the time they are far away from their feeding grounds (Hays *et al.* 1999). Under these circumstances we assume that the objective of Ascension Island turtles is to complete the migration alive and in an optimum length of time in order to start feeding again and replenish the energy stores. Animals are expected to follow a strategy that maximizes the efficiency of energy utilisation (Thompson *et al.* 1993), for example, by optimising their swimming performance in order to minimise the energetic cost of migration (Hays *et al.* 1999). Under these premises, by swimming at the minimum COT, those turtles migrating from Ascension Island would minimize their energy expenditure.

Sumich (1983) studied populations of migrating gray whales *(Eschrichtius robustus)*, which are thought to fast during migration, obtaining energy from the oxidation of stored lipids. By swimming at speeds at which COT is minimal (the estimated speed of minimum COT and the speed observed in the migrating animals was nearly identical) gray whales optimised their performance. Ascension Island green turtles do probably fast, we can therefore predict that 2.59 km/h (mean speed of migration observed), is probably the speed at which the COT is minimum, allowing them to optimise the energy expenditure.

It seems obvious that a large amount of fat reserves would be advantageous when facing long distance migration whilst fasting. It is difficult to ascertain whether or not other green turtle populations feed during migration. If this is the case and do not fast and/or do not perform long distance migrations, greater body sizes are expected to be found in green turtles from Ascension Island as compared to green turtles from other locations. This is because of the large amount of energy required to face the migration fasting. In fact, the average Curve Carapace Length (CCL) for nesting green turtles is 99.1 cm (Hirth 1980) and the mean CCL of the turtles studied in this work is 112.3 cm. Furthermore, looking only at the individuals of Ascension Island, it can be hypothesised that larger body sizes may be beneficial to individuals within the population.

Performance of long dives during migration

Individuals achieve great energetic savings if they choose to travel submerged as opposed to swimming at the surface during long-distance migrations (Williams *et al.* 2000). By adapting their dive behaviour throughout migration, individuals may conserve energy in order to reach their destination. In this study, we observed a variation in the mean dive duration in relation to the body size. The existence of a relationship between dive duration and body size has been widely reported in the literature, both inter-specifically (see for example Culik *et al.* 1996; Putz *et al.* 1998; Cherel *et al.* 1999) and intra-specifically (Boyd *et al.* 1998; Radl & Culik 1999). However, these studies do usually refer to the ability for large animals to dive longer. The turtles studied in this work showed the opposite tendency: smaller individuals spent more time performing long dives. Large turtles are likely to be able to dive longer than smaller turtles, but by performing short dives and swimming at the minimum COT, they can reach the feeding grounds in a shorter time and start feeding sooner.

As explained above, it seems logical that the turtles would optimise their swimming performance by swimming at their speeds of minimum COT. However, the two smallest turtles (turtles 3 and 11) swam slower than the others, a consequence of performing long dive durations. Dives of such long duration have been reported before in this population of green turtles, in most occasions during the inter-nesting period, and dive duration increased with dive depth, suggesting in some cases the use of resting dives (Hays *et al.* 2001). Williams *et al.* (2000) concluded that greater energetic savings occurred during deep dives (because deeper dives involved a greater proportion of passive gliding through the use of buoyancy). However, by performing long dives and consequently slowing down the overall speed, turtles would make their trip longer and face the risk of not being able to remain alive. So, why do they perform these long dives?

Travelling dives are short and shallow, and the associated metabolic rate is supposedly high, because the turtle is swimming actively (Hays *et al.* 1999). Larger animals have greater energy stores but also higher metabolic rates. The relationship between size of energy stores and metabolic rate is more optimum in larger animals (Schmidt-Nielsen 1972). Thus, small turtles (1) have smaller energy stores and (2) have a less optimum relationship between size of stores and metabolic rate. We can hypothesise that they probably try to swim at the speed of minimum COT, but it is possible that they cannot physically keep swimming continuously all the way to Brazil, having to rest.

Consequences of a change in size

The strategies followed by other migrating animals are diverse, but in general there is a relationship between the size and the behaviour that different animals display, as a result of the energetic costs associated to the migration. For instance, in migratory birds, individuals of higher phenotypic quality migrate and arrive earlier in the season at the mating grounds, in order to get a superior territory and increase the chances to mate. However, Forstmeier (2002) suggested in a recent work that for some species other reasons might be more important that the costs associated with early arrivals, motivating the birds to migrate early. Only birds in good condition are able to survive the costs associated with early arrival (Kokko 1999). Another example is that different bird species with relatively small fat reserves are more likely to perform reverse migratory movements than species with larger fat deposits because they cannot afford to complete the migration in one go (Åkesson et al 1996). Also many migratory birds make large detours to avoid crossing 'ecological barriers' to reduce the energy expenditure (Alerstam 2001).

Optimum flying speed of migrating birds

When looking at the speed of travel we find that migrating birds have traditionally been expected to fly at speeds that minimize the energy expenditure per distance covered (called

Vmr) (as it is expected for sea turtles to swim at the speed of minimum COT). However, Alerstam and Lindström (1990, as quoted in Green and Alerstam 2000) pointed out that in order to minimize overall time spent on migration, including refuelling at stopovers, birds should fly faster than their Vmr. Although there is a possibility that some animals travel at speeds faster than the speed of minimum COT, it is very unlikely for animals performing long distance migration and fasting, because by increasing the energy expenditure they might not be able to arrive to their destination alive. In any case, this is not a common behaviour in birds as appointed by Green and Alerstam (2000) who found in a posterior study Brent Geese flew at speeds close to the predicted Vmr.

Optimum performance of Ascension turtles

In conclusion, as green turtles at Ascension Island probably do not feed, once nesting is complete, turtles must be motivated to finish the migration in the minimal length of time (in order to start feeding again and replenish reserves). On the other hand, there is a limited amount of fat reserves that each individual can use, and this reserve is larger for some turtles than for others. It seems probable that individuals will only rest as little as they need to, or this would unnecessarily lengthen the duration of their migration trip. If the reserves are not large enough to keep swimming continuously at the speed of minimum COT until they reach the feeding grounds, individuals may need to rest probably by performing these long dives. This is what we observe when looking at the results: large animals show a more consistent diving behaviour with, in most cases, an absence of long dives, whereas smaller turtles alternate long and short dives during migration. In conclusion, small animals do perform long dives during migration spending more time to cover the distance between Ascension Island and Brazil, probably because they cannot afford to avoid resting.

Implications of the use of Satellite-Linked Time Depth Recorders

Logistical constraints imposed by the TDRs (Time depth recorders) (it is not possible to recover them from migrating animals) make necessary the use of SLTDRs (Satellite-Linked Time Depth Recorders). However, SLTDRs drawback compression of data (Burns and Castellini, 1998). In this study dive duration was compressed in periods of six hours. Only a mean value of the dive duration was obtained for a six hours period, consequently we can get a good idea of the overall mean dive duration during a certain period of time. However, it is important to keep in mind that we only get information of the general behaviour of the animal and not a detailed description of its performance. Because of these limitations we cannot state that only the two smallest turtles perform very long dives during migration, only that they do it more frequently. It is possible that the other individuals did occasionally stay submerged longer than 20 min, but the information was lost by data compression. For example (see examples A and B in table 4.2 and Fig. 4.5 at page 63), in a six hours period, a turtle could be performing a high number of dives, all of short duration. We would obtain a mean value of short duration and very representative of the behaviour of the animal (example A). On the other hand, if the animal makes one or two very long dives and all the rest of the dives are short, the mean dive duration would be almost the same than in the first case, and useful information would be lost by compressing the data (example B). Besides, sea turtles are animals that spend little time at the surface, generally not enough to send a large amount of data to the satellite. Thus, by compressing data, the time spent at the surface is usually enough to send compressed information, although occasionally the information contained in the oldest six hours periods can be lost. A significant relationship between the mean dive duration and the speed at which the turtles travel was observed. However, since detailed information of the dive duration (complete dive profiles), is not yet available for migrating sea turtles the understanding of their diving behaviour and its influence on the speed have still some gaps. We cannot ascertain that the larger turtles of this study do not perform long dives, but we can say that even if they do, the percentage of time spent performing these dives is considerably less than for smaller animals.

Direct effect of body size on the speed of travel

There may also be a direct effect of body size on the speed of travel that is independent of the duration of the dives. For instance, Putz *et al.* (1998) studied several species of penguins, and observed a tendency for larger species to swim faster than smaller ones. This direct effect on speed cannot be directly concluded from the results. However, the direct influence of body size on the speed of travel, if any, would be expected to be small since it was not found to be significant in the analysis.

Number of dives

Besides dive duration, another aspect of the diving behaviour can significantly influence the speed of travel: the number of dives performed. The fewer number of dives performed, the greater the speed of travel. Equally, the larger the size of the individual, the lesser the number of dives performed. This means that, if the number of dives in a given cell is low, then the horizontal distance covered is great. Dive duration and the number of dives are closely related. If dive duration increases (i.e. when turtles perform resting dives), the number of dives will be large too.

Effect of the oceanic current on the swimming speed

I have suggested that the studied individuals modify their diving behaviour in order to optimise their energy expenditure. Their overall performance is, then, greatly influenced by intrinsic factors such as their fat reserves. By optimising their diving behaviour, they can make a better use of their limited energy stores. However, other factors, which must be taken into account when studying marine animals, are the oceanic conditions they face during migration.

The main current that green turtles from Ascension Island encounter on their way to the Brazilian coast is the South Atlantic Equatorial Current (see chapter 3). I mentioned earlier that these turtles follow a direction close to the one of this ocean current for the majority of the migration. Luschi *et al.* (1998) suggested that these turtles could be using the ocean current as a cue for orientation during their migration. This study has shown that the relationship between the speed of the current and the speed of the turtles is not linear. However, there is an increase of the speed of the turtles when they are following the direction of the current (i.e. when the angle between the two directions decreases). If the turtles benefit from travelling within the prevailing current, they will be expected to do so for as long as possible, in order to reduce their energy expenditure. Hays *et al.* (1999) showed, for this population of green turtles, that three of the tracked individuals had changed direction at some stage during their migration trip in order to head in a West-North West direction, which consequently increased their velocity. This is consistent with the results of the present study as a significant relationship between directions and speed has been shown.

Conversely, we observe that when the angle between the turtles' directions and the ocean current's direction increases, the corresponding speed of travel decreases. If the individuals do not follow the same direction as the oceanic current, their overall energy expenditure is very likely to increase as a result of this, as they would not benefit from the effects of the ocean current. If we assume that the main objective of the turtles is completing their migration by optimising energy expenditure, their overall behaviour will be orientated to reach this aim. The possible behaviours green turtles can adopt in order to migrate more efficiently have been described in the present study, for example swimming at their speed of minimum COT or making use of ocean currents.

Speed through the water

Migrating birds increase their airspeed when flying against a head wind (Pennycuick, 1982). Similarly, they reduce their flying speed when they can benefit from the wind speed and direction. This way, they optimise their energy expenditure by taking advantage of the wind (Pennycuik, 1978). Some marine animals do also benefit from currents. For example adult plaice (*Pleuronectes platessa* L.) probably use selective tidal stream transport to optimise energy expenditure during migration (Metcalfe and Arnold, 1990). Unlike birds and plaice, the results of this work show that Ascension Island green turtles do not change their swimming activity (speed through the water) with changes of the current. It is possible that while swimming from Ascension to Brazil they cannot distinguish the variation of speed of the current. Another explanation is that if the turtles decreased the speed of travel at high current speeds they would reduce their energy expenditure by taking advantage of the current, but this would also lengthen their migration.

Other factors that could affect the speed of travel

When looking at the results we see that the duration of dives, the number of dives performed and the angle of the turtle with the current explain 51.79% of the variation of the observed speed of travel. Therefore, there must be other factors, which can affect the speed of the individuals. Since green turtles are ectothermic animals, we can hypothesise that the sea surface temperature can affect their diving behaviour, which could result in a variation of the speed of travel. Hays *et al.* (2001b) compared the routes followed by some of these turtles with the sea surface temperature, and concluded that they did not follow specific isotherms during the migration. Despite the fact that the temperature of the water does not modify their migration routes, the swimming performance of green turtles could be partially affected by changes of water temperature, and it is a possibility that should be considered for future studies. In general, it is difficult to isolate the influence of a single factor on another such as the speed of travel. It is a combination of several factors that will result in the speed at which an animal is swimming at a given time and location.

Malaysian population of green turtles

Finally, I have shown that the relationship between dive duration and speed of travel is not an exclusive feature of the green turtle population from Ascension Island. Indeed, similar patterns are found for a Malaysia population of green turtles (Fig. 4.8 at page 68), although the relationship is not significant for this population (possibly as a result of the small sample size, only five individuals). Migrating green turtles of the two populations swim at a significant different speed. The mean speed of travel for Ascension Island is 2.59 km/h and for Malaysian population is 1.86 km/h. Turtles within the Malaysian population follow very different routes unlike Ascension Island turtles. It is possible that during migration they do not benefit from the effects of currents. On the other hand, the swimming speed at which the COT is minimal could be lower than the one for Ascension Island turtles, maybe as a result of a smaller size. In any case, these are questions that would need a longer study to answer and should be consider for future studies in order to clarify the behaviour of migrating green sea turtles.

CONCLUSIONS

The conclusion of this work is that diving behaviour and oceanic currents are the main known factors influencing the speed of travel of Ascension Island green sea turtles. Because Ascension Island turtles are believed to fast, we can expect that they will optimise their swimming performance during migration in order to successfully achieve their final destination. By swimming at the speed at which COT is minimal, turtles could optimise their performance. Large fat reserves may allow larger individuals to complete the migration by swimming actively, while small individuals do probably need to rest during migration by performing long dives.

During migration Ascension Island green turtles do benefit from the prevailing current, increasing the speed of travel when swimming in the same direction than this.

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