Movements and diving behaviour of post-nesting green turtles (<italic>Chelonia mydas</italic>) in the South Atlantic Ocean and the Mediterranen Sea.

Richardson, Sallyann

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Movements and diving behaviour of post-nesting green turtles (*Chelonia mydas*) in the South Atlantic Ocean and the Mediterranean Sea

Sallyann Richardson B.Sc., M.Sc.

Swansea University
Prifysgol Abertawe

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To my family

Summary:

This thesis investigates the movements and diving behaviour of free-ranging green turtles (*Chelonia mydas*) using data obtained by attaching satellite transmitters onto ten individuals from two distinct populations of nesting turtles in the Mediterranean Sea (n=3 individuals) and Atlantic Ocean (n=7 individuals). Dive profile data was obtained for the first time for green turtles in the Atlantic Ocean. The migration routes, speed of travel and diving behaviour were examined during different phases of the post-nesting behaviour. The location data were analysed to investigate the effect of filtering on the perceived turtle movements. All turtles were found to maintain distinct home ranges once migration ceased and the size of this home range was found to be significantly related to the water depth, with deeper turtles utilising larger areas.

The diving behaviour was found to support the findings of previous studies of migrating and internesting green turtles with a high proportion of time spent conducting either shallow travelling dives or midwater dives. Activity sensors confirmed that turtles actively swim during midwater dives and do not passively ascend as previously thought. Speed of travel was found to be significantly related to diving behaviour with turtles travelling faster when conducting a higher proportion of shallow dives. Overall travelling speed was not found to be related to turtle size.

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………13-03-2009……………………………

STATEMENT 1

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

Signed….. ……………(candidate)
Date………13-03-2009……………………………

STATEMENT 2

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

Signed… ………………(candidate)
Date….13-03-2009…………………………………

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Thesis development:

My work on green turtle (*Chelonia mydas*) migration began as a short study for an MSc dissertation. I was presented with a data set from transmitters attached to 3 nesting green turtles in the Mediterranean Sea which had been stored as a print out and needed transference back onto computer. As the unravelling of this huge data set began, patterns emerged of clear differences in behaviour during the post-nesting migration back to foraging areas. It then became apparent that seasonal behaviour could be identified for the first time as the transmitters worked for long enough to pick up over wintering 'hibernation'. It became clear that 3 months was not long enough to glean all the information from this data set and hence continuance of this work formed the first stage of my MPhil studies. After solving software problems, temperature data could be extracted from the satellite results and by digitising the bathymetry of the area, the behaviour changes over winter could be compared with temperature cues and changes in sea depth. This lead to collaboration with Dr BJ Godley and publication of these results in *Ecography* in 2002 (Godley et al., 2002). Further investigation helped me find methods to overcome problems associated with satellite-derived location data allowing accurate routes to be identified and small-scale movements and home range to be described. I then worked on determining speed of travel from such data sets to compare it to diving behaviour.

In 2001, I travelled to Ascension Island in the South Atlantic and assisted in the attachment of 7 satellite-relay data-loggers to nesting green turtles. These transmitters had not been deployed on turtles before but had already allowed location data and dive profiles to be collected from seals (e.g. McConnell et al., 1999; Fedak et al., 2001, 2002). The hope was to collect information on dive behaviour of green turtles migrating back to Brazil from Ascension Island- one of the most remarkable migrations seen in this species. Previous earlier technology had identified routes and patterns in behaviour from summaries received during migration and it was hoped that collection and transmission of dive profiles would lead to more understanding on the type of diving undertaken during such a long migration. The transmitters continued to work once the turtles reached Brazil and allowed us to study the behaviour as the turtles travelled along the coast and ceased movements in foraging areas. The routes were published in *Animal Behaviour* in 2002 (Hays et al., 2002b). By using analytical procedures I had developed when examining the Mediterranean data set, I then set about elucidating behavioural patterns from this new data set. As the remarkable migration undertaken by this population of green turtles in the South Atlantic is so energetically demanding, I hoped to understand more about the migration strategies seen here and the importance of travelling in the most cost efficient way.

Outline of thesis:

This thesis is presented in 6 chapters:

Chapter 1: **Introduction.** This chapter reviews the current knowledge on green turtle diving behaviour and the technology used to further understanding.

Chapter 2: **Foraging areas of green turtles (*Chelonia mydas*) in the Mediterranean Sea and the implications of using satellite telemetry results.** This chapter is a separate study carried out towards the beginning of my studies looking at the Cyprus data set to understand the methodology necessary to accurately describe results obtained from ARGOS location data and also be aware of its limitations.

Chapter 3: **Methods.** The scientific methodology used to examine the Mediterranean and Ascension Island data sets is explained in detail in this chapter. I explain the format of data received from the different transmitters and how this is processed. I also explain in more detail how speed of travel is calculated and the diving behaviour analysis.

Chapter 4: **Location data; migration routes, swimming speed and home range.** The results are divided into two sections due to the volume of data presented. In the first chapter, the location data provided by the transmitters is examined in detail. I describe the amount of data received, the post-nesting migration routes and the calculated speed of travel. The home range is also analysed once the turtles cease migration.

Chapter 5: **Diving behaviour: dive profiles, changes during migration and at foraging grounds.** In the second results chapter, all aspects of the diving behaviour are presented. The first section of the chapter explains how the dive profiles are defined into dive type. The quantity and quality of dive data received are presented, the diving behaviour for each phase of migration is described and also compared with the speed of travel during the oceanic phase. The dive profiles are compared between foraging and inter-nesting and diurnal patterns are investigated.

Chapter 6: **Discussion.** In this chapter, I discuss the relevance of the results obtained and compare the different populations examined in this study. I also examine how the diving behaviour provided by the SRDLs compares to previous studies of Ascension Island turtles.

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I am very especially grateful to Jonathon Houghton and Corinne Martin from the Swansea research group for all the feedback and advice offered during my studies. I would also like to thank my examiners Professors Tim Guilford and Rory Wilson for their extremely useful feedback.

Finally, a big thank you to all my family for their support.

CHAPTER 1

General Introduction

1. Introduction.

Satellite telemetry is becoming an increasingly used tool to remotely study marine animals whilst they are at sea (French, 1994; Block, 2005; Godley et al., 2007). This study examines diving and location data obtained from two populations of green turtles using different technology and aims to discuss the possibilities and limitations of such data sets with respect to insights into marine animal behaviour. Aspects examined include the movements of the turtles after nesting and the implications of using satellite-derived locations which require the application of filtering methods for a more accurate picture of the range and movements of the animal. Also, the diving behaviour is studied in order to add to the understanding of life history strategies of marine turtles and the behavioural choices made in different areas depending on the phase of the breeding season and associated energy constraints.

1.1. Study species and life history:

Green turtles (*Chelonia mydas*) are one of eight species of marine turtle that inhabit the world's seas and oceans. They are widely distributed in tropical and subtropical waters, near continental shelves and islands, and are rare in temperate waters. Their normal latitudinal range remains within the northern and southern limits of the 20°C isotherm, and follows the seasonal latitudinal changes of these limits (Marquez, 1990). In this thesis, data sets were obtained from studying green turtles from two distinct regions, the eastern Mediterranean Sea and the South Atlantic. The major reproductive aggregations of green turtles in the Atlantic basin and Mediterranean Sea together comprise over 20,000 nesting females per year (Encalada et al., 1996). Green turtle nesting habitat is widespread over the tropical and warm temperate region, and tagging data indicate that movement of breeding females between geographically separate colonies is extremely rare (Meylan, 1982). Studies of mitochondrial DNA show distinctive evolutionary lineages for Mediterranean and South Atlantic rookeries. In the Mediterranean, only the green and loggerhead turtle (*Caretta caretta*) are known to nest (Venizelos et al., 2005). It is estimated that as few as three to four hundred green turtles now nest annually and they are considered as regionally endangered (Broderick et al., 2002). Interaction with fisheries is thought to constitute a real threat to marine turtles in the eastern Mediterranean as they are caught as bycatch and are seen as detrimental to the livelihood of fishermen as they may damage nets, spoil the catch, or remove bait (Godley et al., 1998). The main nesting areas in the Mediterranean for this species are Cyprus and south eastern Turkey with feeding grounds off the North African and Turkish coasts.

Brazilian coastal waters have been seen as an important foraging and travelling area for turtles that nest in many different countries. Tagging studies initiated in 1958 first showed the long distance migration of nesting green turtles from Ascension Island to foraging grounds off the coast of Brazil (Mortimer and Carr, 1987). Green turtles tagged in the Guianas have also been recovered in tropical Brazil (Pritchard, 1976). Large numbers of juveniles also feed in these waters due to the abundance of macroalgae in this region (Godley et al., 2003). But in this area marine fisheries have been seen to impact on turtles, with incidental capture in nets placed perpendicular to the shore. In recent years, however, Project Tamar, an organisation set up by the Brazilian government and Institute of the Environment, protects over 1100 km of the country's coastline (Marcovaldi and Marcovaldi, 1999). In the South Atlantic, the majority of the data for this study comes from adult green turtles that shuttle between nest sites on Ascension Island and foraging grounds off the Brazilian coast. Also included in the analysis are data obtained from juvenile green turtles released after accidental capture by coastal artisanal fisheries off Brazil. As these individuals were captured at sea, it is unknown which nesting population they would belong to.

Green turtles are an example of a species that spends different portions of its life cycle in clearly defined separate habitats (Figure 1.1, p. 5). The majority of a green turtle's life is spent at sea. When the hatchlings emerge on the nesting beach, they scramble straight down the shore to the sea. They swim directly offshore and then remain at sea, until, a few years later, juveniles settle in shallow coastal areas where they remain until they mature. Once mature, the turtles migrate every 2 or 3 years to nesting areas, where breeding takes place and the females come ashore to lay 3 or 4 times, with about 2 weeks in between each nesting event. After nesting, the turtles swim back to the foraging areas where they remain until ready to breed again.

A fundamental problem for anyone studying a migratory species such as the green turtle is as different portions of the lifecycle are spent at spatially separated locations, it is highly likely that different behaviour will be undertaken at each of these. Optimal foraging strategies may vary depending on changes in food resources in different habitats (e.g. leatherback turtles (*Dermochelys coriacea*) in the North Atlantic change dive depth and diel periodicity as they travel depending on prey abundance (Hays et al., 2006)). If there are no foraging opportunities available, behaviour will then be governed by energy conservation. Marine turtle studies are almost exclusively conducted at nesting areas, with diving behaviour recorded using data storage tags

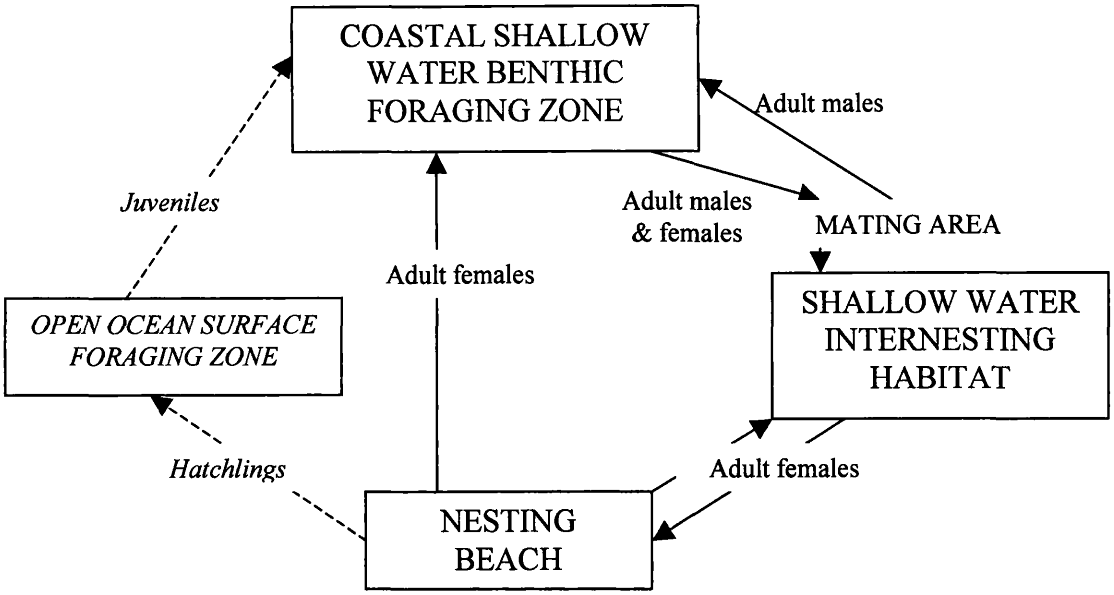

Figure 1.1: Life history and temporal distribution of the green turtle. (Redrawn from Miller, 1997)

which must be physically removed. Studies are concentrated at nesting areas as the turtles come ashore to lay their eggs and data storage tags can be attached during one nesting event and retrieved during the next (Godley et al., 2007). But this encompasses a very short time scale in a turtle's life and relatively little is known about where they go and their behaviour in-between nesting seasons. The migratory behaviour of turtles has been looked at in more detail since the discovery of long transoceanic migrations across the Atlantic and the return of female turtles to the same nesting beach time after time. Although the orientation of hatchlings can be studied in artificial conditions, the study of the migration and cues used by adult turtles during long distance movements are best understood by tracking the animals at sea. Now that satellite transmitters can include devices to measure depth and time, the actual diving behaviour can be seen as the animal moves through the sea (e.g. Fedak et al., 2001; Godley et al., 2002; Hays et al., 2004).

It is important to understand the habitat use of marine turtles because of their potential effects in the dynamics of nearshore marine ecosystems (Heithaus et al., 2005). Also, studies on foraging grounds have proved important for understanding growth and mortality factors that effect demography. For example, mortality on feeding grounds appears responsible for a decline in nesting populations of loggerhead turtles along the Queensland coast (Limpus et al., 1994) and human-inflicted mortality of green turtles on feeding grounds in the Caribbean appears to have major consequences for population stability and growth (Bjorndal et al., 2003).

1.2. Technology used in marine turtle studies:

With an increase in the interest in marine animal tracking, technology is continually advancing to allow more data to be collected for longer periods of time and with increasing reliability and accuracy (Godley et al., 2007). With links between behavioural and oceanographic studies, the use of marine animals as instruments to measure variables at sea is leading to a whole new avenue of science. The Tagging of Pacific Pelagics (TOPP) program alone has employed 2000 transmitters on 22 different species since 2000. (For a detailed review on sea turtle satellite tracking, see Godley et al., 2007.)

There are two types of transmitters deployed on green turtles in this study that provide location data and information on diving behaviour. The first transmitters attached in 1998 were Wildlife Computers tracking units (SDR-SSC3, Wildlife Computers Redmond, WA, USA), which provided dive information as 6 hour summaries in histogram bins. These transmitters also provided temperature data as 'time-at-temperature' histogram bins. The transmitters attached in 2001 were the series 7000 Satellite Relay Data Loggers (SRDLs) manufactured by the Sea Mammal Research Unit (SMRU, St Andrews, UK). An onboard microprocessor determined the time and depth of the five most marked points of inflection during each dive and from these dive profiles could be reconstructed (Fedak et al., 2002; Myers et al., 2006). Due to limited bandwidth of the satellite system, profiles were stored and transmitted at random when the animal surfaced, so an entire record was not received.

Mark-recapture studies first showed that green turtles make long-distance movements between nesting grounds and foraging areas. Female green turtles that were tagged at nesting beaches on Ascension Island were captured on the Brazilian coast 2000 km away (Mortimer and Carr, 1987). Then in 1997, 6 post-nesting green turtles were tracked from Ascension Island to Brazil using the Argos satellite system (Luschi et al., 1998). Researchers received up to 5 locations per day and were able to calculate the distances travelled and hence the swimming speed of the turtles. The first attempt to track a turtle in the Mediterranean by satellite recorded location data for a single loggerhead turtle (*Caretta caretta*) (Hays et al., 1991). From the proportion of satellite fixes obtained, it could be inferred if the turtle was spending more or less time at the surface during certain times of the study. In a more recent study, green turtles nesting in Cyprus were equipped with time-depth recorders (TDRs) and activity sensors that monitored internesting diving behaviour and activity (Hochscheid and Wilson, 1999). They obtained data that enabled them to identify highly variable diving patterns and extensive foraging periods. The data was sufficient to separate the proportion of time spent travelling, foraging and resting during the internesting period. Studies using TDRs on Ascension Island green turtles have also shown different diving behaviour and enabled diel patterns to be recorded (e.g. Hays et al., 1999). Time-depth recorders are evolving all the time with increased memory capacity and power supply in miniaturised forms. Many studies now use continuous-recording equipment enabling dive profiles and ascent and descent speeds to be presented in detail. These tend to be used for short-term experiments due to the huge amount of data they collect (e.g. recording diving behaviour during the internesting interval (approximately 12 days) for green turtles at Ascension (Hays et al., 2000) and loggerhead turtles in Cyprus (Houghton et al., 2002)). Many recorders are designed to become unattached from the animal after the study so that the data can be recovered from the recorder (e.g. van Dam and Diez, 1996; Hays et al., 2000a), rather than relying on satellite transmissions, which are a drain on the battery supply and limit the amount of data that can be received (Fedak et al., 2002). Satellite-linked time-depth recorders encode and compress dive data so the information can be received in satellite transmissions along with a location fix over a relatively long study period, in some cases for over a year (e.g. Hays et al., 2006; Broderick et al., 2007). Using remotely gathered data is advantageous because the data are available whether or not the recorder is recovered from the animal but it has meant that data must be compressed and much detail is lost.

In recent years GPS technology is being adapted for use on marine species. An important tool in studies of terrestrial and aerial species (Hulbert and French, 2001), it was unsuitable for tracking marine vertebrates as surfacing times are generally too short to acquire sufficient satellite signals. However, by calculating positions during post-processing, fine-scale movement patterns have now been obtained for loggerhead turtles in the Mediterranean Sea (Schofield et al., 2007). Such accurate location data could then be overlaid on GIS maps identifying critical habitats for conservation and previously unrecorded movements by these turtles into near-shore shallow water habitats. This technology is often still limited by the need to physically retrieve the logger from the animal although satellite-linked GPS transmitters are beginning to show excellent potential for recording detailed movements (Yasuda & Arai, 2005). New ‘Fastloc’ technology (which acquires GPS constellation signals within a fraction of a second) is being trialled in loggerhead turtles off the North American coast and also shows great promise for gathering data on free-ranging marine animals (Godley et al., 2007).

1.3. Home range and location data:

Chapter 2 discusses in detail the ARGOS system and how locations are received remotely from study animals. The effects of location filtering on home range analysis are examined with respect to the population of turtles in the Mediterranean Sea. In this thesis I also aim to describe the movements of the turtles tracked in the South Atlantic and apply the techniques investigated in chapter 2 to study their home range once they cease long distance movements and become resident off the Brazilian coast.

1.4. Migration behaviour and speed of travel:

The mean dive duration of migrating turtles has been related to speed of travel (Tomillo, 2002). In this thesis I want to compare the travelling speed as the turtles migrate to the type of diving behaviour seen in order to try and understand more about migration strategies.

The speed at which an animal travels is dependent on a variety of factors. All animals have a range of speeds which they are capable of travelling at (Wickler et al., 2000), but the actual speed is determined by the medium they are moving through, the size of the animal, its shape (Williams and Kooyman, 1985), the gait (Wickler et al., 2000), physiological constraints (Williams et al., 1993), and behaviour (e.g. Culik et al., 1994). For marine animals, long distance travel is often an important part of their life cycle. Seasonal cycles lead to a change in day length, temperature and food availability, and many animals have different requirements of a habitat for different portions of their life cycle. This will therefore necessitate transit between different sites. Often these journeys are undertaken on routes where foraging is unavailable and hence must be carried out solely on stored energy supplies. For example, Californian grey whales (*Eschrichtius robustus*) migrate up to 20,000 km each year spanning 50° of latitude from summer feeding to winter breeding grounds. They are forced to fast for 4-6 months relying on stored lipid reserves during this time (Sumich, 1983). Another example is seen in the green turtles that migrate over 2,000 km from South American feeding grounds to Ascension Island to nest (Luschi et al., 1998). It is assumed that they cannot feed during the open ocean journey nor at Ascension (Mortimer and Carr, 1987) and must therefore adapt their behaviour to minimise energy consumption during a period of many months (Prange, 1976). Migrating animals, which rely on stored energy supplies, must minimise their energy expenditure and optimise the utilisation of stored fat in order to successfully swim long distances. Travelling in the most cost-efficient way and moving at speeds as close as possible to their optimum cost of transport (CoT)[1] (Fish, 1982) are important factors in determining the actual swimming speed of the animal. Thus, animals may travel at a preferred speed which minimises the overall use of energy and not necessarily the maximum speed the animal can swim at (Prange, 1976). For example, if a green turtle travelled at its maximum swimming speed of approximately 7.2 $km.h^{-1}$, the return journey between Ascension Island and Brazil could be completed in around 27 days, but this would required stored fat reserves 3 times the actual body mass of a turtle. Consequently, for a long migration, energy use will be much more important than the overall time taken.

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[1] Cost of Transport can be defined as the amount of energy (in joules) required to transport 1 kg of body mass over a distance of 1 m ($J.kg^{-1}.m^{-1}$) (Schmidt-Nielsen, 1972).

Marine air-breathing animals, including turtles, are constrained by the necessity to return to the surface to breathe. It is not efficient to swim along at the surface because a considerable amount of mechanical energy is wasted generating surface waves (Hertel, 1966). Moving animals experience drag and to move through a medium (air or water) requires overcoming this drag force (Hind and Gurney, 1997). Water is 800 times denser and 60 times more viscous than air (Williams, 1999) and hence drag is a very critical factor governing speed when moving through water. Hydrodynamic drag consists of forces created by frictional, pressure and wave drag (Vogel, 1994). Frictional drag is due to the distal thickening of the thin boundary layer of fluid around the animal as the water passes over it, pressure drag is due to the shedding of vortex sheets during forward movement and wave drag becomes a factor as the animal swims at the surface and produces a wake. All these forces vary according to variables such as the shape and size of the animal and its travelling speed (Hind and Gurney, 1997). The more streamlined an animal, the less drag it will experience (Williams and Kooyman, 1985). Long migrations are a dominant part of the life history of marine turtles and their morphological, behavioural and physiological adaptations are related to efficient, long-distance movement through the water (Wyneken, 1997). They are highly streamlined compared to semi-aquatic and freshwater turtles (Davenport et al., 1984). The gait of marine turtles is also adapted for powerful efficient swimming. Marine turtles swim using a 'powerstroke', rowing with the fore-flippers only in such a way that the upward and downward strokes both provide thrust (Wyneken et al., 1994). Freshwater turtles use a different stroke that allows better manoeuvrability but not such fast forward motion (Davenport et al., 1984). Foraging turtles use this gait when speed is not important but are seen to switch gaits as soon as longer distances are to be covered.

Drag forces have been shown to be maximum just below the surface and then decrease down to a minimum at a depth equal to 3 times the body diameter of the moving object (Hertel, 1966). Deeper than this, the animal does not produce surface waves meaning that total drag is minimal. Some air-breathing animals minimise this effect by behavioural strategies such as porpoising - jumping in the air where drag is much less important than in the water (Hui, 1989). Dolphins approach the water surface at speed and leap clear of the water during ventilation to reduce the cost of high-speed swimming (Williams et al., 1993). Wave-riding and adherence to a narrow range of routine swimming speeds also decrease the amount of energy expended when pinnipeds and cetaceans move near the water surface (Williams, 2000). For semi-aquatic animals, surface-swimming has been shown to incur higher costs of transport than that of any submerged swimmer (Prange, 1976). For example, the muskrat (*Ondatra zibethicus*) swims at the surface and shows a minimum CoT 13.5 times greater than a similarly-sized fish (Fish, 1982). Sea otters (*Enhydra lutris*) have distinct speed ranges associated with different modes of travelling, and when conducting sustained surface swimming, they are much slower and have a higher rate of oxygen consumption than when swimming fully submerged (Williams, 1989). Due to their behaviour when swimming, marine turtles cannot avoid the high drag layer at the surface. At each breath the turtle ceases swimming and uses the flippers to raise the head above the water surface (Prange, 1976), thus reducing the overall speed of travel. Satellite transmitters have shown that travelling turtles spend a high proportion of time conducting short, shallow dives (Balazs et al., 1994; Hays et al., 2001a). Once a breath is taken, they swim down to a depth of around 3 times their maximum body thickness (approximately 2 m) and swim along at this depth for a few minutes before swimming back up to the surface again (Hochscheid et al., 1999). In this way they avoid spending time near the surface as much as possible but do not waste time diving down to deeper depths where differences in drag are negligible (i.e. more than 3 times their maximum body thickness). This strategy of travelling dives is consistent with predictions for optimising energy efficiency during migration when feeding en route is not possible.

Other animals in transit are seen to conduct deeper dives, for example, grey seals (*Halichoerus grypus*) perform 'V-shaped' dives when in transit between haul out and foraging sites diving down to or close to the seabed or in deeper water to hundreds of metres (Thompson et al., 1991). This is assumed to be in order to survey the water column and seabed for potential opportunistic foraging, not an option for green turtles that do not feed in the open ocean as it is unsuitable habitat for their food (Bjorndal, 1997). Their herbivorous diet means that suitable foraging areas are in warm, shallow coastal waters. When turtles are migrating along shallow coastlines it is seen that their speed is lower than open sea travel. Studies using satellite transmitters have shown that this is due to longer dives inferred to be foraging or resting dives (Papi et al., 1997). Longer dives have been recorded during open sea migration of green turtles (Balazs et al., 1994; Hays et al., 1999). These longer dives have been suggested as midwater resting dives and have been more commonly seen at night. They tend to be around 19 m in depth and it is assumed that at this depth the turtle achieves neutral buoyancy and hence expends little energy remaining submerged at this depth (Minamikawa et al.., 2000). It is also thought that they would not float on the surface to rest because of the risk of predation. A turtle floating on the surface of the ocean would be clearly silhouetted to any predators such as sharks swimming below.

Diving behaviour has been seen to have a close relationship with the travelling speed of marine animals. Northern elephant seals (*Mirounga angustirostris*) exhibit a strong negative relationship between dive duration and swimming speed (Le Boeuf et al., 1992). Marine animals would be expected to employ aerobic metabolism and avoid longer dives when travelling as anaerobic metabolism is much less efficient. The aerobic dive limit depends on oxygen stores and the activity levels. Transit-swimming dolphins move near the surface and maintain constant stroking (Williams et al., 1999). Short duration dives permit greater flexibility of speed as oxygen store limitations are not a problem, whereas during long dives they must employ more energy-conserving strategies (Williams et al., 1999). In species that dive during horizontal travel, movements and migrations to foraging areas are most efficient when time underwater is maximised due to the highest energetic cost of swimming occurring close to the surface. Seals can spend as much as 90% of their time at sea submerged (Thompson et al., 1993). Tracking of migrating marine turtles shows that over 90% of time is spent submerged (for example, Hays et al., 1999; Gitschlag, 1996; Renauld and Carpenter, 1994). Migrating green turtles in the French Frigate Shoals engaged in short dives close to the surface (Balaz et al., 1994) and they were only at the surface for 4-5% of the time. Migrating turtles travelling back to Brazil from Ascension Island travelled mainly at 0.9-1.5m depth (Hays et al., 2001a). They travelled faster during the day than at night when they engaged on deeper dives.

Many studies that track marine animal movements use speed of travel to make inferences about behaviour. It is seen as diving behaviour changes so travel speed changes. For example, when elephant seals travel at speeds greater than 0.4 ms^{-1}, they conduct mainly 'V-shaped' travelling dives, whilst at slower speeds they conduct mainly pelagic foraging dives (Le Boeuf et al., 2000). The transit dives maximise the distance covered and seals can employ behaviour like gliding to minimise the cost of travel (Williams et al., 2000). Swimming speeds are slower when seals are foraging as they have to balance the relative costs of different swimming speeds with the advantages a particular speed may confer with the efficiency of catching prey- as swimming speed during foraging directly affects prey encounter rates (Thompson et al., 1993). Adélie penguins (*Pygoscelis adeliae*) swim for approximately 1 min below the surface before breathing with a normal cruising speed (when carrying externally attached data loggers) of 2.2 ms^{-1}. This then drops to 1.5 ms^{-1} when engaged on searching and feeding dives (Culik et al., 1994). Underwater swimming accounts for 73% of the travelling time. Satellite tracking of travelling Humboldt penguins (*Spheniscus humboldti*) showed two peaks in the range of travelling speeds, the first was 1.8 ms^{-1} which is around the normally seen underwater speed, whilst the second was around 3 ms^{-1} which has been observed as the speed during porpoising behaviour (Culik and Luna-Jorquera, 1997). Grey whales travel at a mean velocity of 2 ms^{-1} but observers have recorded speeds of less than 1 ms^{-1} when whales were courting or avoiding boats (Sumich, 1983). Low speeds indicated resting and foraging activities of Antarctic fur seals (*Arctocephalus gazella*) whilst deeper dives and faster travelling speeds were seen between the colony and foraging events (Bonadonna et al., 2000). McConnell et al. (1992) tracked foraging trips of grey seals. They foraged opportunistically on the outward journey and lower swimming speeds were seen than on the return journey. The swimming speed for the minimum cost of transport was estimated at 1.2 ms^{-1}, speeds were only seen around this when the seals were in transit. When the speed dropped the seals were assumed to be foraging.

At present there are a limited number of cases where satellite tracking has followed the entire migratory journey of marine turtles from nesting beaches to resident foraging areas (e.g. Papi et al., 1997; Cheng, 2000). Turtles that nest on mainland beaches may simply migrate along the coast back to foraging areas, with for example, loggerheads on the coast of southern Africa travelling 500-1000 km along the Mozambique coast between nesting and foraging areas (Papi et al., 1997). Other populations of turtles that nest on small isolated islands require a certain amount of open ocean crossing to return to their foraging areas, for example, some green turtle populations migrate between Hawaiian islands (Balazs et al., 1994). But one of the most remarkable examples of such an open ocean crossing is the green turtles that migrate from the South American coastline to Ascension Island in the middle of the South Atlantic (Luschi et al., 1998). The journey of approximately 2000 km takes about 60 days of continuous swimming. For some populations, the migration route involves both open sea and coastal migration, and often it can be noted that the open sea stage follows a very direct route back to the mainland before the coastal leg of the journey. For example, green turtles in the Penghu Archipelago of Taiwan migrate across the open sea and along the mainland of China (Cheng, 2000). Any increase in coastal migration may be assumed to be advantageous as the turtle can engage in opportunistic feeding before returning to their home area, even if this results in a longer journey overall (Cheng, 2000). Open ocean crossings followed by coastal migration have not yet been studied in detail but it would be expected that if foraging became available once in shallower water, then the turtle would slow down and engage in longer dives to the sea floor. Thus a reduction in speed would be seen when comparing open ocean and coastal migration.

The aim of this section of the study is to examine the diving behaviour and speed of travel as these turtles migrated and to; (1) consider how filtering the locations provided by Argos can lead to a more accurate description of the speed of travel, (2) investigate if the speed of travel is related to the diving behaviour of migrating green turtles, (i.e. see if there is a correlation between how fast the turtle is swimming and the amount of time spent engaged on dives of a specific depth and duration, and if this correlates with predictions on travelling in the most cost efficient way), and (3) examine any differences seen between open sea and coastal travel and discuss inferences that can be made on the turtles behaviour as a result.

1.5. Dive behaviour, depth and duration:

Previous studies using time-depth recorders, that take measurements every few seconds to reconstruct a complete record of diving behaviour (e.g. Rice et al., 1998), have indicated that green turtles carry out a highly variable dive pattern but certain dive types can be distinguished with distinct profiles. Whilst conducting open sea migration, green turtles have been seen to engage in midwater dives; diving down to around 15-20 m depth and then gradually ascending for a high proportion of the dive before a period of rapid ascent at the end of the dive. These have been hypothesised as resting dives (Minamikawa et al., 1997) or turtles remaining at depth for predator avoidance (Hays et al., 2001a), or perhaps energy-saving swimming (Hochscheid et al., 1999). During internesting, green turtles have been found to spend a large proportion of time engaged on dives with a characteristic U-shaped profile - dives where the turtle remains at a fixed depth for a long period of time during the dive (e.g. Hays et al. 2000a). Information from activity sensors employed on turtles nesting on

Cyprus suggests that some of the U dives were resting dives, whilst others showed benthic activity (Hochscheid et al., 1999). Around Cyprus, foraging opportunities exist, whilst in comparison at Ascension there are none and all the U dives are therefore assumed to be for resting as energy conservation is so important here. During studies of diving behaviour using TDRs on juvenile foraging green turtles, U-dives (dives to the seafloor for resting or foraging activities) are also the most commonly seen dive type (e.g. Southwood et al., 2003; Rice et al., 2000).

TDR studies have identified a change in behaviour of migrating green turtles as they approach shallow coastal waters after a period of open ocean travel, with deep 'S-shaped' midwater dives as if the individual is seeking out the seafloor and then U-shaped dives once a suitable water depth is reached (e.g. Hays et al., 2001a; Martin, 2003). The appearance of these U-shaped dives is often used to signify the end of an oceanic migration. During internesting, U dives can clearly be identified as dives to a uniform depth and of a long duration for resting purposes, but in coastal regions where the turtles can be more active and in shallower water, it is not as straightforward. The challenge with the SRDL data set is to separate the U dives from the individual dive profile record provided for the post-nesting turtles and then try and describe the behaviour that these dives are showing. A non-biased method of separating dive types is necessary, especially when turtles enter shallow water and dive shapes may not be as definite as in deeper areas.

When cameras and data loggers were simultaneously deployed on green turtles in a coastal habitat it was noted that a variety of behaviours can be reflected in one specific dive profile (Seminoff et al., 2006). Previously it had been assumed that dives with bottom phase depth fluctuations were foraging dives (e.g. van Dam and Diez, 1996) and U shapes dives were for resting purposes (e.g. Hochsheid et al., 1999). Video footage however revealed that benthic foraging and horizontal movements also produced U-shaped profiles and therefore care must be taken not to assign behaviour simply by time-depth plots.

Studies on foraging green turtles in coastal regions have shown that they spend the majority of time engaged in two types of dives; foraging and resting (e.g. Brill et al., 1995; Davis et al., 1999). They are distinguishable by submergence time; during foraging turtles are active and therefore dives are short as oxygen is consumed quicker. Also, as the turtles tend to be at shallow depths when feeding, less air may be taken in or the turtle will be positively buoyant and utilise a large amount of energy simply staying underwater (Minamikawa et al., 1997). During resting, the turtle tends to stay submerged for longer periods of time and at greater depths where they can be neutrally buoyant with a larger volume of air in the lungs (Hays et al., 2000a). Many turtles show a diel pattern of different dive types throughout the day, often with peaks of foraging behaviour during mid-morning and mid-afternoon, with resting in between (Ogden et al., 1983; Bjorndal, 1980). A few populations have been observed to feed during the night but either when there is bright moonlight or in areas where human disturbance limits feeding during daylight hours (Bjorndal, 1980; Ogden et al., 1983; Balaz et al., 1984).

Temperature is the principle environmental factor influencing the daily activities of terrestrial animals (Cloudsey-Thompson, 1961 in Schmid et al., 2002), whereas due to high thermal capacity of water, daily temperature fluctuations are minimised in the aquatic environment. As a result, the ecological significance of diel patterns in aquatic animals is less clear, but probably related to predation and food acquisition. Many different species of marine vertebrates show diel foraging behaviour (e.g. penguins (Wilson et al., 1993), killer whales (*Orcinus orca*) (Baird et al., 2005), leatherback turtles (Eckert et al., 1989), and basking sharks (*Cetorhinus maximus*) (Sims et al., 2005)). For some it will depend on the behaviour patterns of their prey. Galapagos fur seals (*Arctocephalus galapagoensis*) that feed on zooplankton show different day and night diving behaviour due to vertical migration of their prey (Horning and Trillmich, 1999). Leatherback turtles dive to different depths depending on the deep scattering layer (Eckert et al., 1989). Studies of diving behaviour in Antarctic fur seals (*Arctocephalus gazella*) reveal a close relationship between diving depth, time of day and the vertical distribution of their main prey (Croxall et al., 1985). This suggests that in order to minimise foraging effort, feeding is conducted mainly at night when prey is nearer the surface. Other species that depend on visual observations to catch prey will forage during the day and rest at night. Northern rock hopper penguins (*Eudyptes chrysocome moseleyi*) (Cherel et al., 1999) and Adélie penguins (*Pygoscelis adeliae*) forage either exclusively or mainly during the day (Wilson et al., 1983). This implies their foraging is restricted by the necessity of sufficient light to see their prey. Sometimes potential predators on a species will be more active at certain times of the day and hence they avoid foraging during this time. Spinner dolphins (*Stenella longirostris*) in coastal Hawaiian waters typically spend daytime hours in very shallow areas, apparently to minimise predation by sharks (Norris et al., 1994). Pan-tropical spotted dolphins (*Stenella attenuata*) also showed a distinct difference between day and night dive behaviour (Baird et al., 2001).

One of the fundamental differences between diving reptiles compared to diving mammals and birds is their difference in metabolism (Hochschied et al., 1999). The low rate at which oxygen is utilised in reptiles enables them to remain underwater for extended periods of time before returning to the surface. The duration of dives can be predicted to vary according to the activity levels of the turtle (Hays et al., 2002c), the dive depth, and the surrounding water temperature. These factors may become more or less important during different times of the year. As temperature affects metabolic rate in turtles, it can be predicted that dive duration will increase as temperature drops. Activity levels can be considered in terms of the oxygen store and how quickly it is used up. A turtle is able to dive with a larger lung volume when diving deeper due to gas compression at depth and hence stay submerged longer (Hays et al., 2000b). Activity levels will affect the metabolic rate, and hence a more active turtle will use up this oxygen store more quickly. Differences in activity levels would be expected between foraging areas and nesting areas affecting depth utilisation, dive shape and dive patterns. Predictions can be made regarding the different constraints on behaviour with energy conservation versus optimal foraging strategies.

1.6. Aims of this thesis:

The principle aim of this thesis is to examine two data sets provided by different types of transmitters attached to two distinct populations of post-nesting green turtles to study migration behaviour and speed of travel and then see how behaviour changes once the turtles cease long-range movements. The Mediterranean data set is examined first to extend on published work with respect to the speed of travel and diving behaviour relationships, location filtering, home range, and diel behavioural patterns.

Then, the conclusions drawn from this study and the techniques developed are used to help analyse the more detailed SRDL data set obtained from post-nesting Ascension Island green turtles.

More specifically, the aims are to:

1) Look at the speed of travel and the corresponding dive behaviour as the turtles migrate across the open sea and discuss how this correlates with predictions on travelling in the most cost-efficient way.
2) Examine the accuracy of Argos locations and then describe the movements and home ranges of the two populations. Do Ascension Island turtles maintain distinct home ranges on their return to Brazil as seen with the Mediterranean turtles?
3) Identify any changes in behaviour associated with arrival at the coast of Brazil and any deep diving behaviour.
4) Try and define profiles into dive type and see if they can be used to delineate between active and resting behaviour simply from the dive shapes or the depth and duration relationships.
5) Discuss the foraging behaviour of the populations and compare with internesting behaviour.
6) Examine the data for diel behavioural patterns and compare these to previous TDR studies of foraging turtles. Do they seem to fit in with other studies that have observed resting at night and foraging during the day?
7) Summarise the use of technology to examine green turtle movements and diving behaviour.

CHAPTER 2

Foraging Areas of Green Turtles (*Chelonia mydas*) in the Mediterranean Sea and the Implications of Using Satellite Telemetry Results

2. Foraging areas of green turtles (*Chelonia mydas*) in the Mediterranean Sea and the implications of using satellite telemetry results.

2.1. Introduction:

With advancing technology, an increasing number of studies of marine animals are relying on satellite telemetry to gather data remotely whilst an animal is at sea. Argos provides a service where transmitters on an animal can send data via a satellite to a ground-based receiving station. The location of the transmitter is then calculated by Argos who compile the information into a database which can be retrieved at any time from any computer with access to the internet (French, 1994). Until recently, satellite-linked transmitters could only provide the location of the animal. Satellite relay data loggers have been developed that can collect data related to the behaviour of the animal and the surrounding environment, as well as providing the location. In order to process data and compare it to the animal's position, Argos has a method of calculating the locations using the Doppler shift of the transmitter signal as it transmits information (Argos, 1996).

Satellite telemetry has been used to successfully record long-distance migrations on many different groups of marine animals, revealing movements only known about previously by tagging and mark-recapture techniques (e.g. Luschi et al., 1998). Such an anecdotal approach can be biased by concentrations of fishing efforts or local biologists and no information is known about the time between marking and recapture (Priede et al., 1991; Plotkin, 1998). With satellite tracking, not only are the destinations known but the journey in between can be followed and behaviour and environmental parameters can be recorded en route. Foraging areas can also be mapped, aiding in understanding food webs and helping with conservation and management strategies (e.g. determining foraging areas of Humboldt penguins (*Spheniscus humdoldti*) to establish commercial fishing limits (Culik and Luna-Jorquera, 1997) and discovering the movements of threatened lesser white-fronted geese (*Anser erythropus*) (Lorentson et al., 1998)).

Although satellite telemetry can reveal long distance movements, the associated error involved with the location calculation means that once small-scale movements are to be examined (e.g. green turtles at nesting grounds or in foraging areas), the accuracy of locations provided by Argos are not usually considered good enough. In marine tracking studies using Argos, locations with a possible error greater than 1 km are most common, hence determining a small home range or small-scale speed measurements would involve a lot of possible errors. For small-scale studies in permanent foraging areas, radio or sonic tracking is a preferred method due to increased accuracies depending on the skill of the operator (e.g. Starbird and Hillis, 1992; Bull, 1995) and where possible visual observations are made (e.g. Houghton et al., 2000; Ogden et al., 1983). Long-term studies of this type are not possible for reasons of cost and logistics as the tracker must remain close to the subject animal at all times. When studying large migrations, for example, California gray whales (*Eschrichtius robustus*) (Sumich, 1983) or black-browed albatrosses (*Diomedea melanophris*) (Gremillet, 2000), where the study animal travels a total of thousands of kilometres at speeds of 170 km and 450 km per day, respectively, errors of 1 or 2 km will not appear as much deviation on the route. If an animal is residing in a small bay or travelling along a coastline at a slower speed, errors of 1 km could give locations inland or out to sea drastically affecting any home range or speed of travel calculations.

When Argos records a location, it assigns a level of accuracy, or location class, based on the number of uplinks and the quality of the transmissions. These location classes (LC) are 3, 2, 1, 0, A and B. Argos transmitters send uplinks (radio signals) on an extremely stable ultra-high frequency to polar-orbiting NOAA satellites. Locations are determined from the Doppler, or frequency, shift as the satellite passes over the transmitter (Mate, 1989). There are different classes of location data; designation is determined by using parameters such as the spread of messages during the pass, the pass duration, and the transmitter velocity (Argos, 1996). At least 4 successive uplinks are required in order for a location to be determined during an overpass that is LC 0, 1, 2 and 3. Only 3 uplinks will allow a location of class A and, if only 2 successive uplinks are received, a fix of location B will be provided. Argos provides predictions of the errors of 3, 2, and 1 but no guarantees are given for 0, A or B. In studies where enough locations are received of LC 1, 2 and 3, the other points are discarded, but in most animal tracking studies few LC 3 or 2 fixes will be achieved, especially for tracking at sea. Satellite telemetry relies on uplinks being received by the satellite and this can only occur when a marine animal is at the surface, as transmissions will not pass through seawater. As marine animals do not tend to be at the surface for very long, LC 0, A and B will dominate. Argos does not predict the accuracy of these latter classes and speed of travel is often used as a filtering method (e.g. McConnell et al., 1992). If the speed of travel between 2 points is biologically unrealistically high then one point is simply discarded from the analysis (e.g. Barlow and Croxall, 2002; Hull et al., 1997; Luschi et al., 2001). For example, many studies examining green turtle migration behaviour use the threshold swimming speed value of 5km h^{-1} as the cut-off point following Luschi et al. (1998), where this value was derived from speed values calculated using high accuracy localisations only.

Keating (1994) decided that using a method of simply filtering locations by Argos LC or speed between consecutive points was flawed and came up with a new index of location accuracy using vectors and angles. The reasoning was that large errors are more likely where data indicate a single, relatively large movement, followed by an immediate return to a point near the origin, and less likely when data indicate localised movements, movements in unrelated directions or successive movements in the same direction. This method will discard any points from long-range short-term movements, a problem if sampling frequency is low and if animals were making any frequent long-range forays from a central point.

As Argos transmitters become more widely used, studies on the location accuracy of individual transmitters highlight differences between the errors that are predicted for each location class by Argos and the actual distances seen (see table 2.1, pp. 29-30). Methods include testing in fixed positions before deployment (e.g.Vincent et al., 2002; Boyd et al., 1998) or, in studies where the position of the animal can be verified by other means, the known location is compared with that provided by Argos to calculate the error (e.g. seals in haul-out sites (le Boeuf et al., 2000), or comparisons with GPS readings when the animal is sighted (e.g. Burns and Castellini, 1998)). Location accuracy is a function of many interacting factors; it is affected by platform terminal transmitter (PTT) elevation (significant in studies of high-flying birds), velocity and frequency stability (affected by temperature shifts), the number and

				Latitude						Longitude					
	Transmitter type	**n**	**Study animal/site**	**3**	**2**	**1**	**0**	**A**	**B**	**3**	**2**	**1**	**0**	**A**	**B**
Argos (1996)	-	-	-	0.150	0.350	1	>1	-	-	0.150	0.350	1	>1	-	-
Keating et al. (1991)	Telonics ST-3 PTT	10	Unobstructed site on animals	0.361	0.903	1.188	12.090								
Vincent et al. (2002)	SMRU Satellite data relay loggers	4	Juvenile grey seals	0.157	0.259	0.494	2.271	0.762	4.596	0.295	0.485	1.021	3.308	1.244	7.214
Hays et al. (2001b)	Telonics ST-10 & 14 PTT. 750g	9	Fixed location	0.12	0.28	1.03	4.29	1.39	5.23	0.32	0.62	1.62	15.02	0.81	7.79
"	"	"	"	0.27	0.54	1.33	10.1	0.99	7.0						
Burns & Castellini (1998)	SLTDR (wildlife computers ver 3x)	11	Weddell seal pups			4.1 (mean)	8.8 (mean)					2.5 (mean)	5.5 (mean)		
"	"	"	"			5.4	20.3								
Goulet et al. (1999)	SLTDR (wildlife computers)	2	Grey seals			1.335	43.799								
McConnell et al. (1992)	SMRU transmitters.	65	Grey seals		1.022	2.238	3.792								
Stewart et al. (1989)	-	42	Harbour seals		1.1	1.7	15.1								
Brothers et al. (1998)	-		Shy Albatross				4.1	8.6					13.3	6.2	
Britten et al. (1999)	PTT-100 satellite transmitters (microwave telemetry) 30g	11	Rock doves				11.5	6.8	98.5						
Boyd et al. (1998)	SMRU PTT (1.5kg)	24	Antarctic fur seals	0.957	0.362	1.082	2.587	42.604	43.926						
Mate et al. (1997)	Satellite monitored radio tags	9	Northern right whales				7.5								
Rodary et al. (2000)	PTT (telonics) with VHF transmitter. 260g	8	Fixed position and Penguins at colony	0.691	0.930	1.436	5.687	3.330	16.904						
Hull et al. (1997)	Telonics ST-10 Transmitters. 80g	10	Royal penguins	1.0 (mean)	1.0 (mean)	1.0 (mean)	7.0 (mean)	9.0 (mean)	4.0 (mean)	0.6 (mean)	0.9 (mean)	1.0 (mean)	8.7 (mean)	14.9 (mean)	4.6 (mean)

Table 2.1: Examples of errors reported when using satellite transmitters on animals. Table shows the transmitter type and study animals or site for each reference, and the reported errors (in km) that were used when examining location data (divided into latitude and longitude whenever this was stated in the reference). Figures are assumed to be standard deviation unless otherwise stated. (Values in blue and bold are straight-line errors and not described as latitude and longitude separately).

temporal distribution of messages received by the satellite, the distance of the PTT from the satellite ground track and satellite position error (sunspot activity) (Keating et al., 1991). As the size of the transmitter decreases, the PTTs become less accurate. For example, using miniature bird tags leads to greater errors due to frequency instability from a greater variability of tag temperature (Britten et al., 1999).

Location error is generally found to be greater in longitude than latitude, resulting in a fixed position in an elliptical distribution of locations with the major axis aligned east-west across the satellite track (Vincent et al., 2002). One exception seen is in a comparison of seal pup locations reported by Argos and determined using GPS, which revealed latitudinal errors greater than longitudinal errors, perhaps due to the high latitude of the study and the time differences between GPS and Argos fixes (Burns and Castellini, 1998). A study at high latitudes is more likely to produce a high magnitude of error due to the low angle of satellite passes and temperature-induced fluctuations of the transmission signal. The Argos 68th percentile predictions refer to latitude and longitude errors separately. Some previous studies have interpreted Argos predictions as referring to the straight-line distance from the true position (e.g. McConnell et al., 1992; Le Boeuf et al., 2000; Wiig, 1995). Studies have also reported their errors in different ways, including; mean straight-line distance from the truth (e.g. White and Sjöberg, 2002), standard deviation of the straight-line error (e.g. Keating et al., 1991), mean latitude and longitude errors separately (e.g. Hull et al., 1997) and standard deviation of these separate errors (e.g. Hays et al., 2001b). Others have considered that the errors reported by Argos are the maximum errors for each location class, i.e. class 3 locations will be within 150 m of the true position (e.g. Paladino et al., 1992; Plotkin, 1998). For general large foraging area and migration studies, not determining the accuracy of fixes in different location classes will not be a serious issue, but once the small-scale movements are more important, location accuracy will play an important role in the interpretation of any Argos received locations.

Here I report on the foraging area movements of three Mediterranean green turtles fitted with satellite-linked time depth recorders or platform terminal transmitters (PTTs). They were attached after nesting to record the post-nesting migrations. The PTTs then continued to work at the foraging grounds providing locations and dive data for up to nine more months. The aim of this study is to look at the locations received by the transmitters at the foraging grounds and assess the feasibility of studying home range and foraging behaviour using this type of satellite transmitter. The specific aims are to 1) understand how location accuracy will affect the interpretation of the results and how other studies have dealt with the errors associated with satellite tracking studies; 2) discuss the size of the home ranges seen here and how they relate to other studies.

2.2. Methods:

The attachment of 3 satellite transmitters (SDR-SSC3, Wildlife computers, Redmond, WA, USA) took place on Cyprus in July and August 1998 (see Godley et al., 2002 for transmitters and attachment procedure).

The location data provided by Argos consisted of a latitude and longitude pair and a location class (see introduction). Various filtering methods were applied to the data to compare the results this produced and what conclusions they would lead to. Location data were filtered using location class, speed between points and the closest 65% to the mean position. If a turtle moved between 2 distinct sites during the study, the data were split accordingly into 2 separate groups for this analysis. The scatter of fixes for each location class was compared with that expected from values predicted by Argos and also those that have been found in other studies where transmitters were tested in fixed positions (e.g. Hays et al., 2001b). The possible home range size for each turtle was calculated.

2.3. Results:

2.3.1. Transmitter performance:

The transmitters worked for between 200 and 282 days at the foraging grounds after post-nesting migration, lasting from arrival at the over-winter sites, throughout the winter and into the next spring (table 2.2, p. 35). The quantity of the locations received varied dramatically throughout the time spent at the foraging grounds for all individuals as they changed locations with the seasons (figure 2.1, p. 36). During the winter months, the number of locations received per day was significantly lower than in the period after arrival at the foraging grounds (table 2.3, p. 35) (ANOVA: $F_{2,1473}=60.89$ $p<0.001$ with a post-hoc Tukey test showing significant difference between the number of locations received per day in autumn, winter and spring.) The time between uplinks became much longer between October and April (mean ± SD for all turtles: before winter, 0.2±0.4d, range 0-2d; during winter, 1.8±3.4d, range 0-32d.)

2.3.2. Location filtering:

Once migration ceased, the fixes received for each of the turtles showed a high degree of scatter, with fixes overland and biologically unrealistic travelling speeds demonstrating that there is error associated with these positions. An example is shown in figure 2.2 (p. 37), where it can be seen that by applying simple filtering processes to the location data for individual 4150, a discrete foraging area becomes apparent for the turtle. By removing all the locations that would require a travelling speed of over 5 kmh^{-1}, the general area where the turtle is residing can be identified (figure 2.2ii). Plotting the closest 65% points (figure 2.2iii), the farthest points are seen to be of

Individual	Time at foraging areas (d)	Total no of fixes	Fixes per day (mean±SD)	Range	No of fixes in each location class 3	2	1	0	A	B
4148	282	266	1.3±1.82	0-7	16	18	28	22	100	102
4149	200	302	1.5±1.92	0-7	7	20	22	22	85	146
4150	270	496	1.8±2.26	0-8	23	46	38	33	130	226

Table 2.2: Quantity of location data received from the attachments during the entire foraging period.

Individual	Phase	Nº days	Locations per day Mean	Range	St.Dev.
4148	Autumn	53	3.9	0-7	1.97
	Winter	105	0.4	0-5	0.88
	Spring	124	1.1	0-6	1.28
4149	Autumn	69	3.6	0-7	1.74
	Winter	98	0.5	0-3	0.85
	Spring	33	0.4	0-3	0.70
4150	Autumn	69	4.4	1-7	1.35
	Winter	112	0.3	0-3	0.68
	Moves	38	0.5	0-3	0.76
	Spring	51	2.7	0-8	2.68

Table 2.3: The number of locations received per day during the different seasons at the foraging areas (all classes). The clear directed movement shown by each individual determines the length of the winter phase.

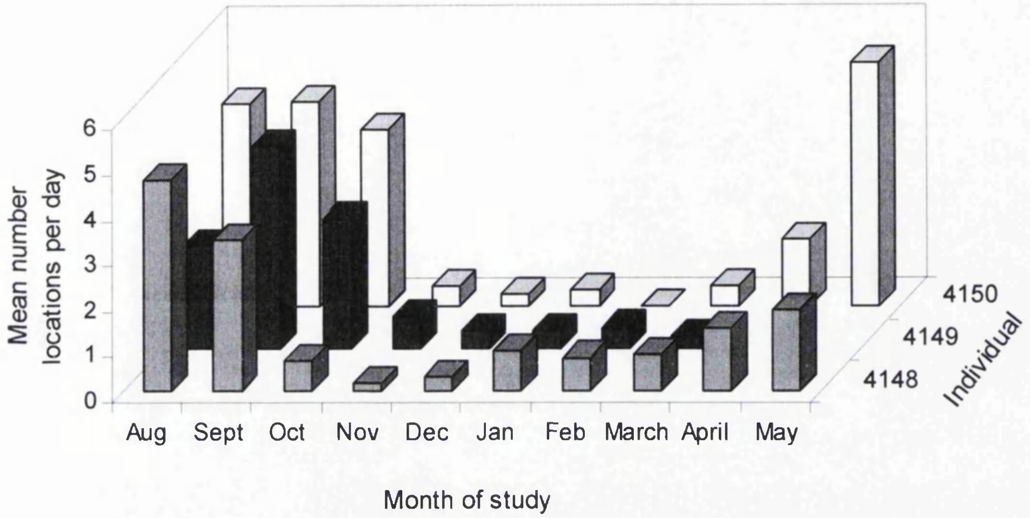


Figure 2.1: Graph showing the mean number of locations received per day for each month of the study.

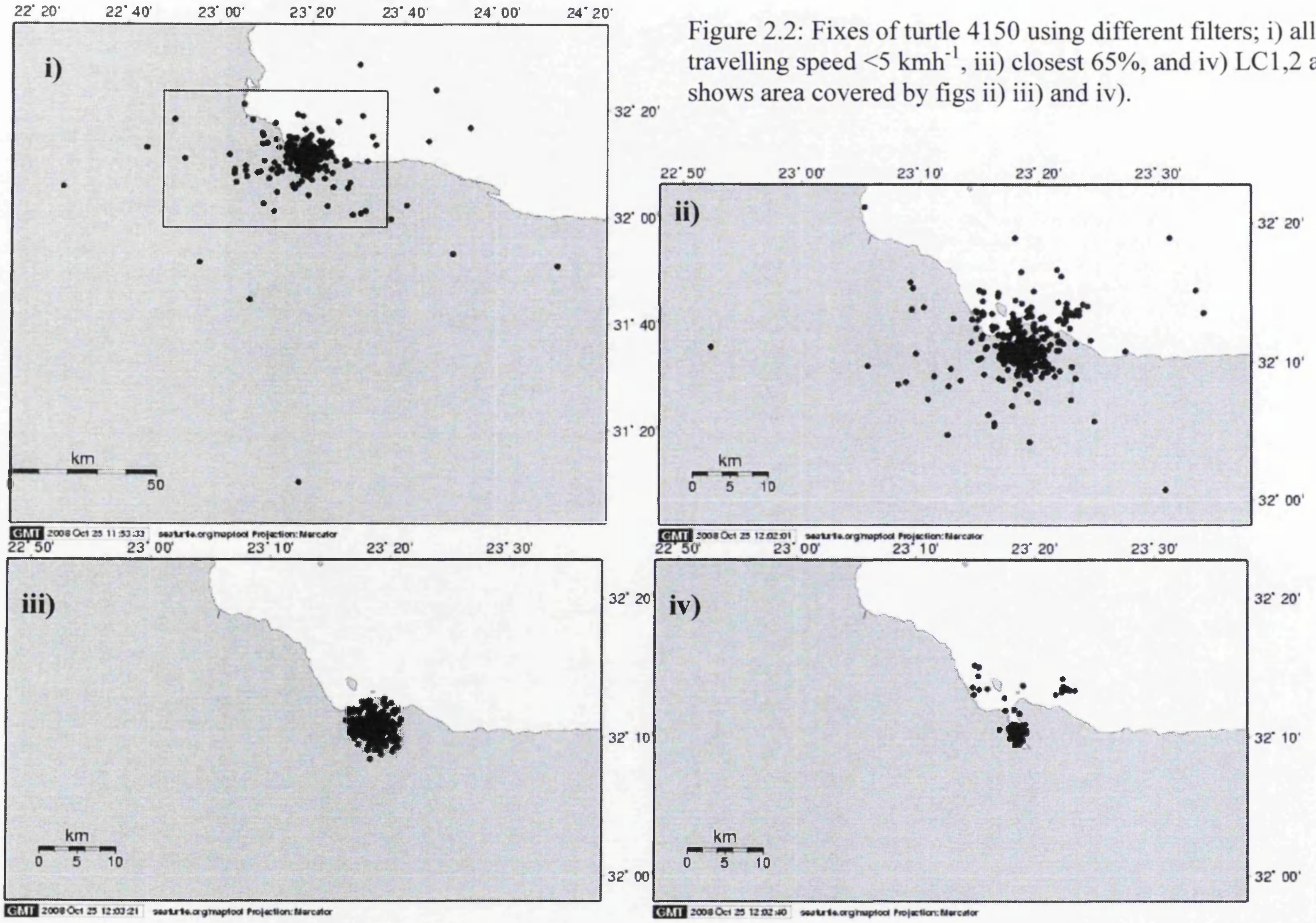


Figure 2.2: Fixes of turtle 4150 using different filters; i) all fixes, ii) fixes with travelling speed <5 kmh^{-1}, iii) closest 65%, and iv) LC1,2 and 3. Box in fig i) shows area covered by figs ii) iii) and iv).

location classes A, B and 0. These show the most scatter around the mean. When discarding all these fixes with the most scatter and simply plotting LC1, 2 and 3, clear areas are seen (figure 2.2iv). (For descriptive statistics see table 2.4, p. 40).

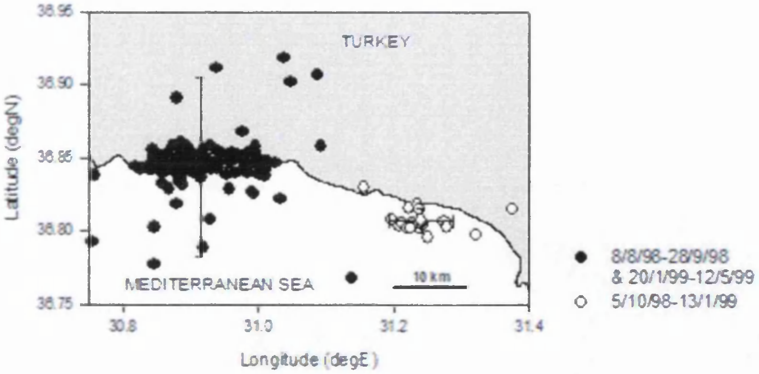
As only the accuracy of location classes (LC) 1, 2 and 3 are described by Argos as being within 1 km of the true position, only these quality fixes have been used when determining the turtles' movements within their foraging areas. Some studies using this technology have found larger errors than Argos predicts (e.g. Hays et al., 2001b; Vincent et al., 2002) but LC 3 and 2 are still within 1 km of the true position and LC1 within 2 km. As the areas covered by these turtles appear to range from 12 km to around 40 km along the coastline, it can be considered reliable enough to describe the turtles' movements using all fixes of all three LC (1, 2 and 3). (For description of the turtles' movements and corresponding maps, see Godley et al., 2002.)

2.3.3. Location Accuracy:

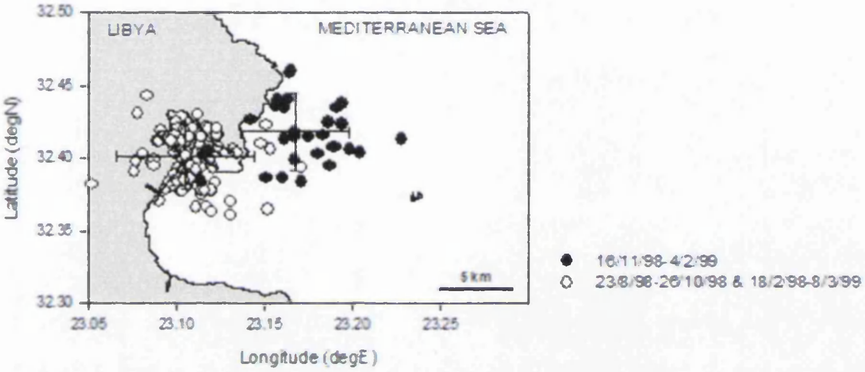
As the turtles spent distinct portions of the study in clearly separate areas, the data were split accordingly for analysis. When locations of classes B and 0 are discarded and the other fixes are plotted there can be seen to be appreciable scatter around the mean position (figure 2.3, p. 39). (For standard deviations see table 2.5, p. 41)

Many fixes are inland and therefore must include a minimum quantifiable portion of error. The distance from the coast is the minimum possible error for each of the fixes considered (table 2.6, p. 42).

i) Individual 4148



ii) Individual 4149



iii) Individual 4150

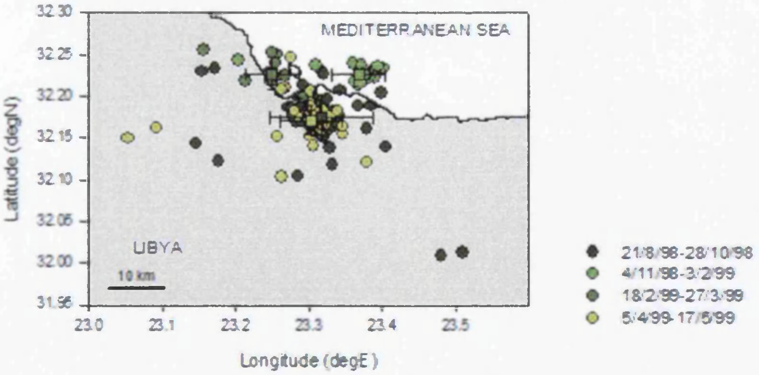


Figure 2.3: Graphs showing all fixes at the foraging grounds of LC A, 1, 2 and 3 divided by seasonal movement. Circles show fixes, square is mean of all locations ± S.D. of all points shown. Solid line indicates the coastline.

			Location Class											
Individual	**Filter**	**Total**	**B**		**A**		**0**		**1**		**2**		**3**	
4148	**All fixes**	**386**	202	*(52.3)*	100	*(25.9)*	22	*(5.7)*	28	*(7.2)*	18	*(4.7)*	16	*(4.1)*
	Speed <5 kmh^{-1}	**337**	164	*(48.6)*	89	*(26.4)*	22	*(6.5)*	28	*(8.3)*	18	*(5.3)*	16	*(4.7)*
	Closest 65%	**251**	101	*(40.2)*	78	*(31.1)*	19	*(7.6)*	23	*(9.2)*	17	*(6.8)*	13	*(5.2)*
	Location class	**62**	0	*(0)*	0	*(0)*	0	*(0)*	28	*(45.1)*	18	*(29)*	16	*(25.8)*
4149	**All fixes**	**302**	146	*(48.3)*	85	*(28.2)*	22	*(7.3)*	22	*(7.3)*	20	*(6.6)*	7	*(2.3)*
	Speed <5 kmh^{-1}	**267**	128	*(47.9)*	74	*(27.7)*	19	*(7.1)*	21	*(7.9)*	18	*(6.7)*	7	*(2.6)*
	Closest 65%	**196**	69	*(35.2)*	74	*(37.8)*	14	*(7.1)*	16	*(8.1)*	18	*(9.2)*	5	*(2.6)*
	Location class	**49**	0	*(0)*	0	*(0)*	0	*(0)*	22	*(44.9)*	20	*(40.8)*	7	*(14.3)*
4150	**All fixes**	**495**	225	*(45.4)*	130	*(26.3)*	33	*(6.7)*	38	*(7.7)*	46	*(9.3)*	23	*(4.6)*
	Speed <5 kmh^{-1}	**431**	183	*(42.5)*	117	*(27.2)*	28	*(6.5)*	38	*(8.8)*	43	*(10)*	22	*(5.1)*
	Closest 65%	**322**	119	*(37)*	103	*(32)*	19	*(5.9)*	26	*(8.1)*	37	*(11.5)*	18	*(5.6)*
	Location class	**107**	0	*(0)*	0	*(0)*	0	*(0)*	38	*(35.5)*	46	*(43)*	23	*(21.5)*

Table 2.4: The number of fixes of each location class used to describe foraging areas for each filter type (as in figure 2.2, p. 37). Numbers in brackets are the percentage of the total number of fixes used when each filter is applied. Corresponds to; i) all fixes received, ii) discarding all fixes that would lead to a travelling speed of over 5km/h, iii) the closest 65% to the mean position, and iv) only plotting fixes of LC1, 2, and 3 which showed the least scatter around the mean.

Individual	**Dates**	**SD of distance from mean (km)**	
		Latitude	**Longitude**
4148	8/8/98-28/9/98 & 20/1/99-12/5/99	7.74	5.66
	5/10/98-13/1/99	7.62	0.79
4149	16/11/98-4/2/99	1.41	1.50
	23/8/98-26/10/98 & 18/2/98-8/3/99	1.33	3.50
4150	21/8/98-28/10/98	1.76	6.14
	4/11/98-3/2/99	0.42	0.45
	18/2/99-27/3/99	1.42	2.69
	5/4/99-17/5/99	1.54	3.00

Table 2.5: The standard deviation of the distance from the mean position for the turtles in the Mediterranean Sea. For each individual, the location data are divided using dates chosen to represent seasonal movement, and then for each of these periods, the latitudinal and longitudinal standard deviation are calculated separately using fixes of LC A, 1, 2 and 3 only.

Individual

4148

		Distance inland (km)		
LC	**N**	**Mean**	**S.D.**	**Range**
0	3	2.08	2.12	0.48-4.48
1	1	1.47	*	1.47-1.47
A	18	4.2	8.2	0.22-35.67
B	85	11.02	26.01	0.44-135.09

4149

		Distance inland (km)		
LC	**N**	**Mean**	**S.D.**	**Range**
0	9	2.103	2.033	0.21-5.17
1	2	2.01	2.55	0.21-3.81
2	1	0.1	*	0.1-0.1
A	16	2.44	6.04	0.15-24.8
B	51	12.89	32.19	0.1-234.67

4150

		Distance inland (km)		
LC	**N**	**Mean**	**S.D.**	**Range**
0	18	5.17	6.36	0.22-17.22
1	2	1.015	1.223	0.150-1.88
2	7	0.3443	0.1513	0.15-0.54
A	51	2.509	3.726	0.11-22.89
B	125	10.76	16.9	0.23-101.41

Table 2.6: The distance from the nearest coastline of all fixes inland for location classes (LC) 0, 1, 2, A and B. (No LC3 fixes were calculated as being overland.)

The fixes were grouped into LC and then the latitudinal and longitudinal distances from the mean were plotted (figures 2.4i-iv, pp. 45-48). This distribution from the mean includes error of the fixes and actual movement of the turtles (table 2.7, p. 49). It appears that longitude has a greater scatter than latitude in an ellipsoid shape around the mean for 4148 but not for 4149 and 4150. (N.B. 4148 resides along an east to west coastline.)

The standard deviation of the distribution of the fixes of each location class minus the standard deviation of the satellite error should leave the standard deviation of the actual biological movement of the turtles and from this the home range could be calculated. As many studies have found a disparity between the longitudinal and latitudinal standard deviation of the error of satellite received locations, they must be considered separately. If the error of each location class was pre-determined before deployment, then the above calculation could be carried out for each location class and the movement of the turtle could be seen using all fixes. As transmitters are known to vary in accuracy, LC3 fixes are considered in this example to represent the true movement of the turtle without any satellite error. Considering LC3 only for locations in the autumn after arrival at the foraging areas, the standard deviation of fixes around the mean is, for latitude; 0.212 km, and longitude; 0.141 km. A macro was created that simulated 10,000 random locations with the same standard deviation as the LC3 fixes (i.e. assumed biological movement component), and then different potential errors (standard deviations) were added until the total standard deviation matched that observed from the Argos locations. This was done for the latitude and longitude of each LC separately hence providing the potential error associated with fixes of LC2, 1, 0, A and B (table 2.8, p. 50).

Assuming LC3 fixes are accurate, the maximum home ranges or foraging areas of the turtles can be calculated. Before and after winter individual 4148 utilised an area within 0.75 by 1.2 km. Individual 4149 used a larger area before winter approximately 1.7 by 5.3 km, whilst 4150 resided in an area approximately 8.1 x 1.2 km before winter.

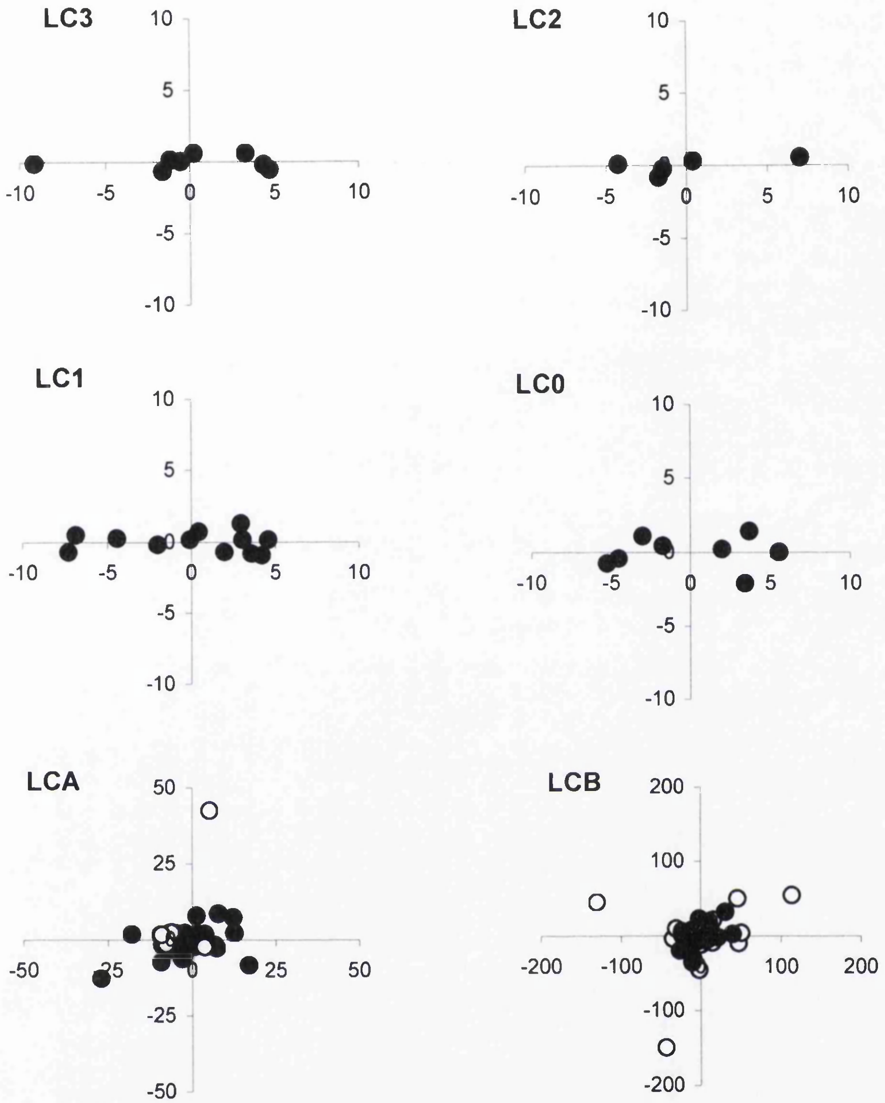


Figure 2.4i: Distance of each fix from the mean position of all fixes in that location class for individual 4148. Open circles show fixes discarded by speed filtering (<5 kmh^{-1}). For dates and descriptive statistics see table 2.7, p. 49.

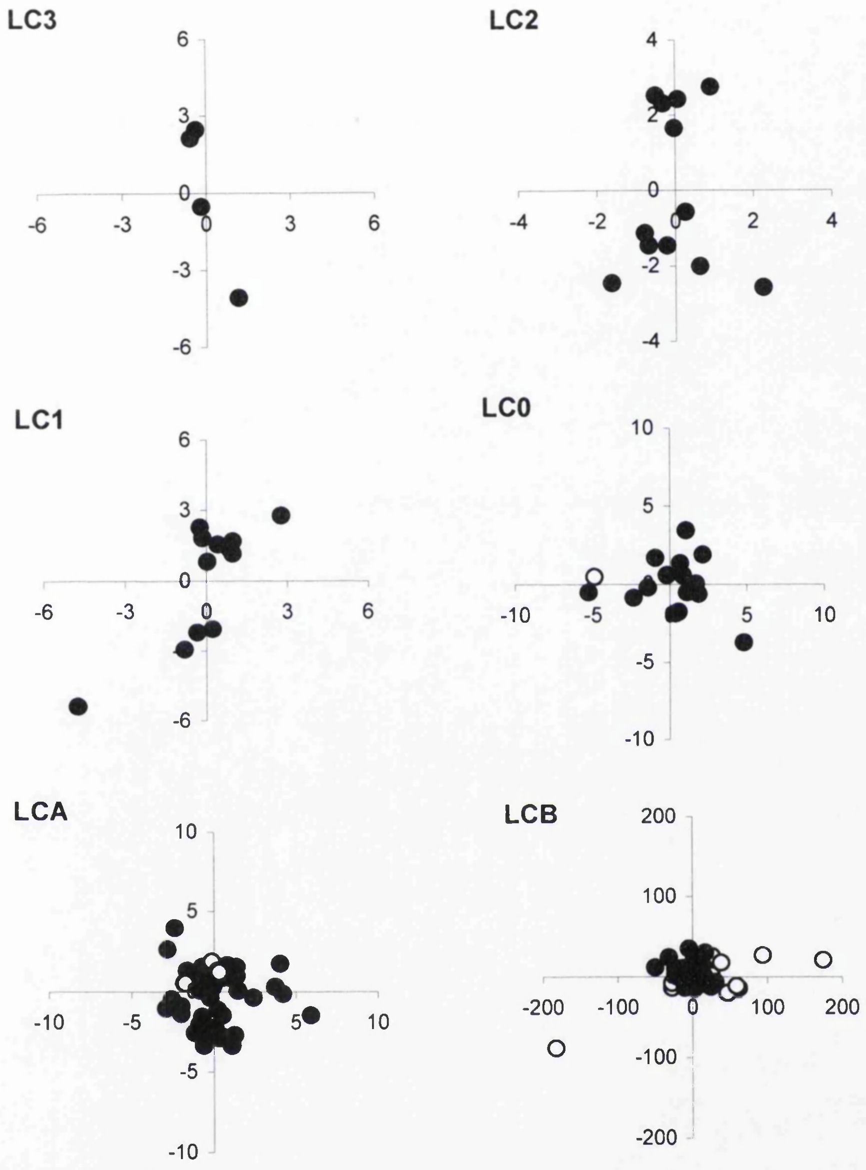


Figure 2.4ii: Distance of each fix from the mean position of all fixes in that location class for individual 4149. Open circles show fixes discarded by speed filtering (<5 kmh^{-1}). For dates and descriptive statistics see table 2.7, p. 49.

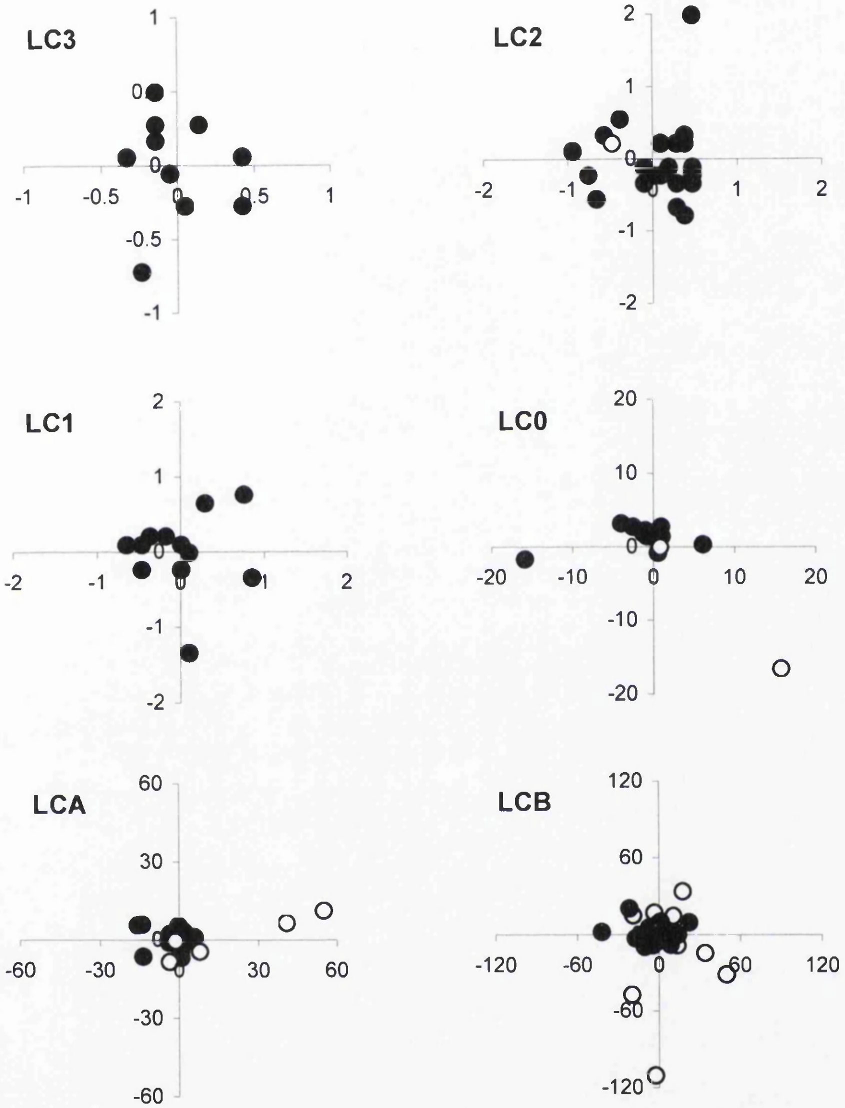


Figure 2.4iii: Distance of each fix from the mean position of all fixes in that location class for individual 4150 during the autumn phase. Open circles show fixes discarded by speed filtering (<5 kmh^{-1}). For dates and descriptive statistics see table 2.7, p. 49. The data are divided into autumn and spring (figure 2.4iv) for individual 4150 as only this transmitter continued to provide locations in the spring.

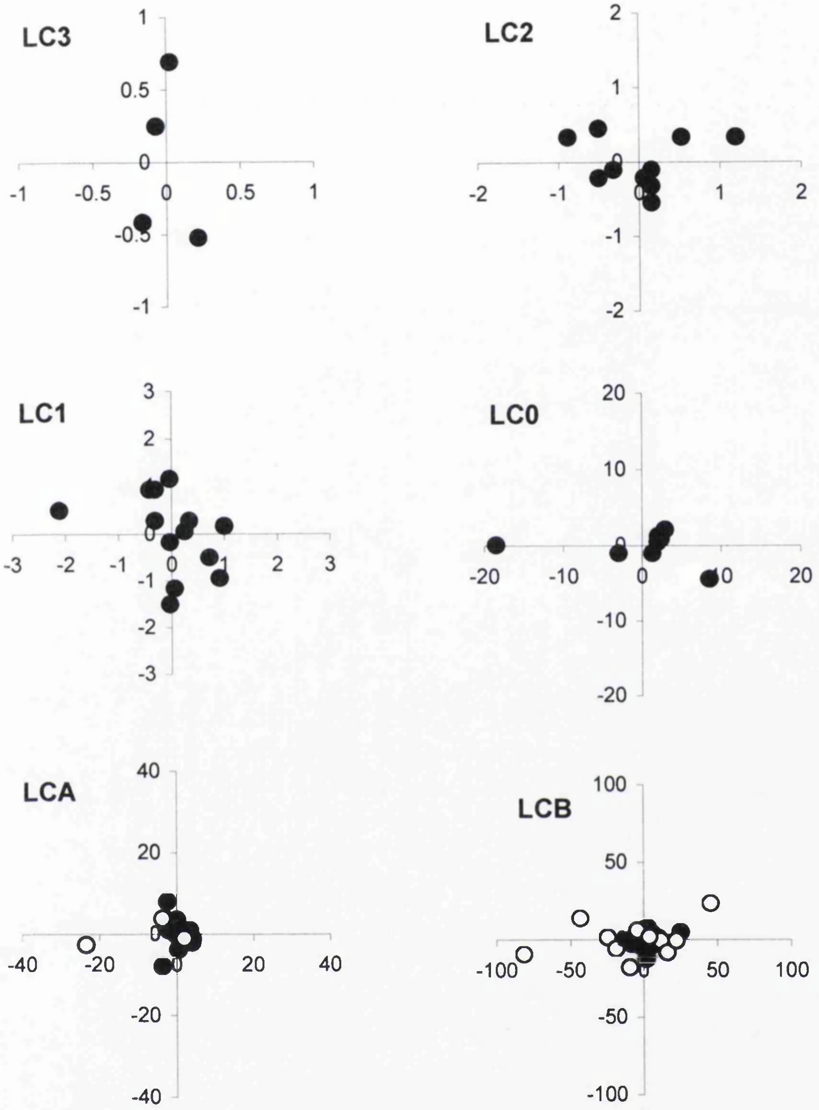


Figure 2.4iv: Distance of each fix from the mean position of all fixes in that location class for individual 4150 during the spring phase. Open circles show fixes discarded by speed filtering (<5 kmh^{-1}). For dates and descriptive statistics see table 2.7, p. 49.

Individual 4148:

LC	N	Long S.D.		Lat S.D.		Straight line Mean ± S.D.
3	8	4.47		0.45		3.21 ± 2.89
2	5	4.26		0.52		3.04 ± 2.62
1	12	4.24		0.69		3.56 ± 2.16
0	8	4.14		1.12		3.80 ± 1.39
A	51	8.95	(7.90)	8.71	(3.75)	7.27 ± 7.15
B	126	20.53	(9.58)	17.63	(7.68)	14.24 ± 22.95

Individual 4149:

LC	N	Long S.D.		Lat S.D.		Straight line Mean ± S.D.
3	4	0.77		3.02		2.37 ± 1.50
2	12	0.97		2.14		2.12 ± 0.80
1	12	1.76		2.56		2.17 ± 1.19
0	16	2.56		1.70		2.53 ± 1.62
A	61	1.62	(1.66)	1.60	(1.62)	1.92 ± 1.19
B	115	29.13	(9.18)	12.36	(7.41)	15.07 ± 27.82

Individual 4150:

LC	N	Long S.D.		Lat S.D.		Straight line Mean ± S.D.
3	**10**	**0.26**		**0.35**		**0.37±0.19**
	4	*0.16*		*0.57*		*0.49±0.18*
2	**24**	**0.44**		**0.54**		**0.57±0.39**
	10	*0.59*		*0.34*		*0.57±0.33*
1	**12**	**0.47**		**0.54**		**0.57±0.39**
	13	*0.78*		*0.83*		*0.96±0.55*
0	**14**	**6.58**	**(5.17)**	**4.95**	**(1.46)**	**4.98±6.42**
	9	*7.53*		*1.94*		*5.14±5.55*
A	**64**	**9.46**	**(3.49)**	**2.82**	**(2.07)**	**4.40±8.81**
	38	*4.29*	*(1.70)*	*2.42*	*(2.42)*	*2.85±3.99*
B	**111**	**9.29**	**(6.59)**	**13.16**	**(3.58)**	**7.81±14.07**
	62	*15.20*	*(4.93)*	*5.36*	*(3.42)*	*8.99±13.47*

Table 2.7: Distance from mean location fix (km), individual 4148: 8/8/98 - 19/9/98; individual 4149: 25/8/98-20/10/98; individual 4150: 2/8/98-25/10/98 (shown in bold) and 29/3/99-17/5/99 (shown in italics). Values in parentheses are the standard deviation if the speed filtered fixes are removed from the calculation (mean not altered).

	Autumn		Spring	
LC	**latitude**	**longitude**	**latitude**	**longitude**
2	0.335	0.185	0.45	0.35
1	0.32	0.255	0.3	0.125
0	0.81	4.45	0.97	4.5
A	1.66	3.1	1.7	3
B	2.8	5.75	2.8	5.8

Table 2.8: The standard deviation of the error of each location class assuming that the LC3 fixes are accurate and represent the true movement of individual 4150 during autumn: 2/8/98 and 25/10/98 and spring: 29/3/99-17/5/99.

2.4. Discussion:

Satellite telemetry is becoming a widely used tool for tracking movements of marine animals. It is logistically straightforward as it does not require observers to follow the study animal at sea, and not only can locations be provided but other variables can be recorded and transmitted via satellite, for example, diving behaviour and temperature (e.g. McMahon et al., 2005; James et al., 2006a). Most species of marine turtle have now been tracked using telemetry to reveal previously unknown behaviour, for example green turtle migration corridors across the Atlantic (Luschi et al., 1998) and South Pacific (Cheng, 2000) and leatherback migrations from the Caribbean (Eckhert, 1998). Transmitters have also showed non-direct migrations from nesting areas to foraging grounds that include open sea and coastal phases allowing opportunistic foraging en route (e.g. Cheng, 2000; Hays et al., 2002b).

2.4.1. Number of locations received per day:

Initial inferences can be made on the turtles' behaviour simply from the number of locations received. In order to calculate a location, the satellite must receive uplinks from the transmitter; this is only possible when the turtle is at the surface. There is window of approximately 10 minutes when the satellite passes overhead (Argos, 1996). If a turtle is engaged in travelling dives of 2 to 3 minutes then it can be assumed that it will be more likely to be at the surface at some point during an overpass than if it is engaged in resting dives of 20 to 30 minutes. However, the dive:pause ratio[2] could also affect the number or accuracy of locations received, as the longer surfacing between dives may provide a greater window for transmissions to the

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[2] The ratio of post-dive surface interval duration to dive duration (Green et al, 2003)

satellite. Thus a high number of good locations during the day means that the turtle is at the surface for more time, fewer locations and the turtle must be submerged for longer periods of time (Hays et al., 1991; Plotkin, 1998). The satellites pass overhead at specific times of the day but as the number of passes does not vary on a daily basis, it can be assumed that the number of locations received per day may be a simple indication of the behaviour of the turtle. For study animals that spend a proportion of time on land and then forage at sea, distinct differences are seen between location uplinks. Culik and Luna-Jorquera (1997) tracked Humboldt penguins (*Sphenicus humboldti*) and concluded that when a low number of daily locations was received this was due to overpasses corresponding to active 'at-sea' feeding phases of the subject animal. When tracking grey seals (*Halichoerus grypus*), McConnell et al. (1992) received significantly fewer locations during foraging trips at sea than haul-out periods. It has been found that the diurnal variation in locations can be highly correlated with satellite visibility (McConnell et al., 1992). The diurnal pattern of satellite coverage is primarily a function of latitude and it has to be noted that this pattern may affect the time of day locations are received as well as the behaviour of the animal. The probability of receiving data from a tag on land is a function of only the satellite pass schedule whilst the probability of receiving a data from a tag at sea is a function of the satellite pass schedule and the time the animal is at the surface (Burns and Castellini, 1998). When satellite tracking king penguins (*Aptenodytes patagonica*), Jouventin et al. (1994) found locations were recorded more accurately during the night than during the day reflecting the difference in dive durations as the penguins were deep-diving in the day due to vertical migration of the prey. Satellite tracking studies on turtles have used the quantity and quality of uplinks to discuss behaviour. For example, a significant difference is found between the number of uplinks during internesting intervals and post-nesting migration, reflecting the activity levels of the turtles (Hays et al., 1999; Plotkin, 1998). Hays et al., (1999) found that locations provided by Argos were received less frequently during internesting of green turtles at Ascension Island (mean 0.92 locations per day) than during post-nesting migration (mean 2.49 locations per day) as a consequence of the longer submergences during internesting. Plotkin (1998) also found accuracy of locations improved during the oceanic migration phase. The turtles spent more time at the surface and for longer periods during each surface interval. In this study, the distinct drop in the number of locations received per day that corresponded with the movement into deeper water during the winter months suggests that the turtles remain submerged for longer periods of time and remain at the surface for short periods only. Before the winter, the mean number of locations received per day ranged from 3.6-4.4, whilst over winter this dropped to 0.3-0.5 (table 2.3).

2.4.2. Location accuracy:

As the satellite received positions are subject to error, it is important to ensure that any movement described actually reflects a change in position by the turtle and is not simply an artefact of the satellite error. When looking at straight-line migrations, for example, an oceanic crossing, extreme observations can be easily observed and removed. By filtering and plotting the locations, it becomes immediately apparent how inaccurate some of the fixes must be. One of the most common methods used is discarding any fixes that would lead to unrealistic travelling speeds. This immediately begins to highlight the foraging area, but still there is appreciable scatter and a high proportion of fixes over land. More accurate filtering methods are therefore needed to accurately determine small-scale foraging areas. If poor quality data is simply removed from the analysis (LC 0, A and B) this can lead to a significant data loss, especially when dealing with tracking studies at sea where an animal may be at the surface for a short period of time leading to fewer uplinks per satellite pass. In this study, that would reject 78-84% of all the location data received from the foraging area. During open sea migration, directed travel means that erroneous locations can be easily defined using a straightness index (calculated as the ratio of the beeline distance and the cumulative sum of all segments of the journey (Butschelet, 1981)) (Hays et al., 2001b; Godley et al., 2002), but once an animal becomes resident in a particular area, this method is no longer applicable. When defining the centre of the home range, often a percentage of locations are omitted to retain the locations that are closest to one another, i.e. those that minimise the total inter-location distance (e.g. Hays et al., 1999; 2001c), although this still does not give an accurate indication of the actual size of the area used. When an animal is close to the coast as seen in this study, the possible minimum error of each LC can be quantified by the distance of inland fixes from the coastline. The results reflect the findings from previous studies of location accuracy that LCB fixes can be very imprecise, up to 235 km from the nearest coastline, whilst no LC3 and relatively few LC1 or LC2 fixes (6% and 10% of the total received for each LC respectively), were reported as inland for any of the turtles.

Other studies of satellite error have found that LCA and LC1 fixes appear very similar in accuracy although transmitters are found to vary (Hays et al., 2001b; Vincent et al., 2002). In this study it appears that there is a lot more scatter in LCA fixes than LC1. The turtle could possibly be moving into these more distant positions, but a high proportion are over land (% of all fixes calculated over land; Turtle A; LC1 3%, LCA 25%; Turtle B, LC1 9%, LCA 21%; Turtle C, LC1 14%, LCA 42%). The mean distances inland are higher for LCA fixes than LC1 fixes with a mean of around 3 km and hence deviations simply from an error of 1 km (predicted by Hays et al. (2001b) and Argos (1996) would still mean that they are being received from a position over land. The results agree with findings that LC3 and 2 are very accurate even if this accuracy is less than Argos predicts. No LC3 fixes were calculated to be in positions over land, whilst the greatest distance inland for a LC2 fix was 0.54 km.

2.4.3. Size of the foraging area:

The energy expended and therefore required by an animal is directly related to its body mass, the time it spends active and the speed of travel (Saunders et al., 1993). An animal's home range can be defined as the area traversed by an animal during normal daily activities, excluding migrations or erratic movements (Bailey, 1984 in Seminoff et al., 2002), and will be a function of its mass (modified by the spatio-temporal dispersion and quality of available resources). A home range contains a finite potential energy resource which is proportional to its area (Lindstedt et al., 1986), with habitats of greater productivity resulting in smaller home ranges (Harestad & Bunnell, 1979). Green turtles are found in the tropics and subtropics around the 20°C isotherm and reside for the majority of their lives in shallow warm coastal areas where algae and sea grass are plentiful (e.g. Balazs, 1980; Bjorndal, 1980; Bjorndal, 1985). Studies on green turtle resident areas have found that they maintain distinct foraging and resting areas (e.g. Ogden et al., 1983). Each turtle has a relatively small foraging area in which plants are cropped which results in fresh plant growth. The home areas of separate turtles tend not to overlap. The turtles that resided off the coast of Libya had much more restricted home ranges than the turtle off the Turkish coast. Turtles 4149 and 4150 both resided in semi-enclosed inlets which would limit the size and movements, whilst turtle 4148 moved along a coastline. It could also be predicted that the waters may be shallower, calmer and warmer in these sheltered bays off the coast of Libya leading to higher productivity and less necessity for movements to find enough suitable food.

If fixes of LC3 alone are considered, Argos predicts that 68% of these points should be within around 150 m of the true position (Argos, 1996), and a study by Hays et al. (2001b) showed their fixes were on average within 270 m of the true position. Bearing this potential error in mind, the least distance moved over winter by any individual was approximately 6 km; this is a lot more than could be attributed to simply error alone and hence must be actual movement by the turtles. When focussing on the details of the home range, fixes of location class 3 indicate small foraging areas with limited movement over long periods of time. This agrees with previous green turtle tracking studies. Foraging green turtles in Kaneohe Bay remained within a 3 km of radius of release point after tagging (Brill et al., 1995). Movement distances of green turtles in a Florida lagoon during the summer months were very similar with an average of 2.6 km (Mendonca, 1983). Food availability would also be an important parameter in determining home range. Green turtles tracked off the coast of Brazil showed a wide range of movements (Godley et al., 2003), and the authors propose a dichotomy of home range size-dependant on whether the diet is predominantly seagrass or algae, with larger home ranges in algal pastures.

By assuming that the standard deviation of the distribution of locations received for each individual is equivalent to the standard deviation of the error associated with each LC plus the actual movement of the turtle, this latter element can be calculated.

Turtle 4150 spent the period before and after winter in the same area, in a semi-enclosed bay where movements can be predicted to be reasonably limited. The distances from the mean location calculated for each LC during both these periods are very similar (table 2.6) which supports the use of this method to calculate the separate standard deviations for the error and the biological movement. By pre-testing the transmitters before attachment, it would have been possible to have had an indication of the error of each location class. When transmitters are deployed on animals at sea, fixes of the more accurate classes (3 and 2) tend to be received only in low numbers. Therefore, by this method, the foraging areas could be more accurately determined using a higher number of fixes including those in less accurate classes. Caution should still be observed when comparing home range size amongst studies when different filtering algorithms have been used. Even so, the size of the home ranges indicated here are comparable to those found by other studies (Brill et al., 1995; Mendonca, 1983; Godley et al., 2003).

2.4.4. Conclusion:

Although this study has provided an understanding of the areas used by these turtles and how the interpretation of satellite received location data can influence the conclusions drawn, only an estimate of the turtles' home ranges can be provided. These results still rely on many assumptions and reinforce the underlying need for tests of satellite transmitters before deployment in order to ascertain the errors associated with each location class for each individual transmitter.

CHAPTER 3

Methods

3. Methods.

3.1. Deployments:

3.1.1: Attachments in the Mediterranean Sea:

Satellite-linked time-depth recorders (SDR-SSC3, Wildlife computers, Redmond, WA, USA) were attached to 3 female green turtles (*Chelonia mydas*) in the Mediterranean Sea where this species is critically endangered. They were attached between July 28th and August 1st 1998 after the turtles nested at Alagadi, North Cyprus (35°33'N, 33°47'E). (For more details of the attachment procedure, see Godley et al., 2002.)

3.1.2: Ascension Attachments:

Between 24th May and 9th July 2001, 7 satellite-relay data loggers (SRDLs) were attached to female green turtles nesting on Ascension Island, South Atlantic (7°57'S, 14°22'W). The satellite transmitters were designed by SMRU, the Sea Mammal Research Unit in St. Andrews, U.K (plate 3.1, p. 60). In order to maximise transmitter longevity, attachments were made at the end of the nesting season (Godley et al., 2001), in the hope that the nesting event during which attachment took place, was the last of the season and the study animals would leave for Brazil within a few days.

The main nesting beach of the island, Long Beach, near Georgetown (plate 3.2, p. 60), was patrolled from about 10 pm each night, until a turtle was noted coming ashore. Using night-vision scopes, she was observed at a distance until she had finished excavating the nest chamber, and after approaching carefully from behind, once eggs

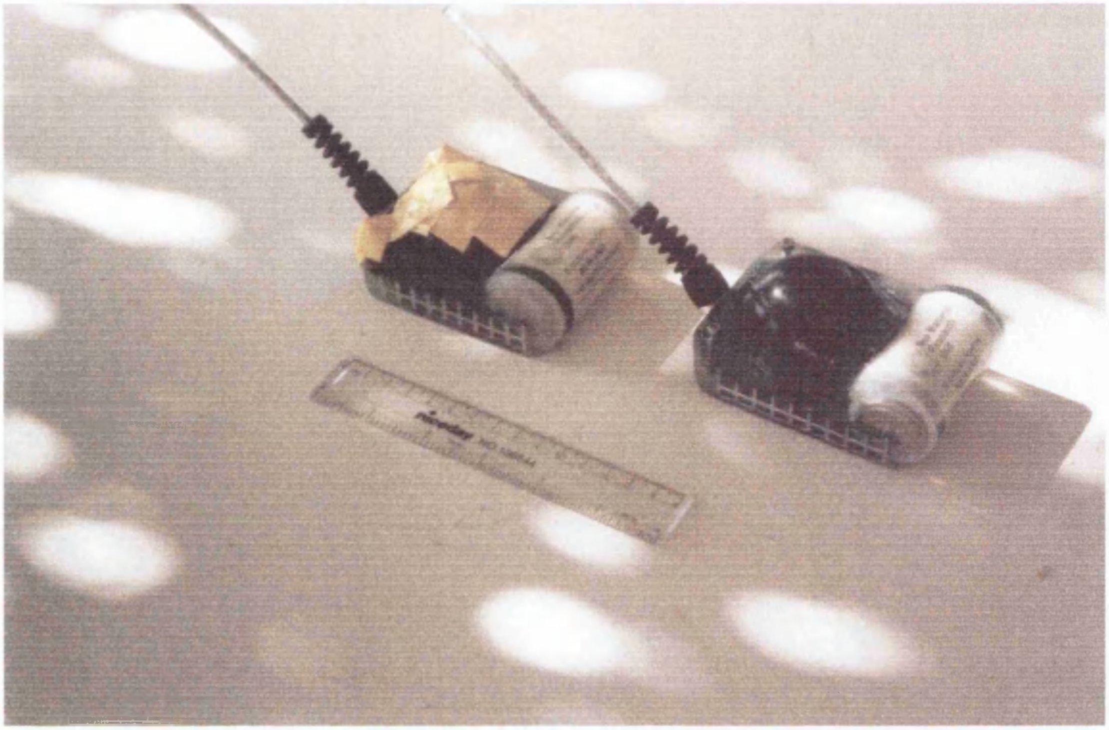

Plate 3.1: SRDL used for Ascension attachment 2001. (The left-hand transmitter has tape over the activity sensor to protect it from excess sand as the turtle covers up the nest. This would then be removed just before the turtle entered the water.)

Plate 3.2: Long Beach, Ascension Island- the main nesting beach on the island.

Plate 3.3: Nesting turtle with eggs visible in the egg chamber. Once the turtle had completed egg laying, the attachment could take place with minimal disturbance to the female.

Plate 3.4: Turtle returning to the sea with SRDL attached.

were seen in the nest chamber, attachment was carried out with minimal disturbance to the female (plates 3.3 and 3.4, p. 61). The shell was wiped with acetone and sandpaper to provide a clean surface to adhere the transmitter to. The transmitter was set in two-component epoxy resin (Foilfast, SFS Stadler, Cheltenham U.K.). The epoxy was moulded around and over the edges of the transmitter to help create a more secure bond and also to create a streamlined outline to the equipment. A small piece of wood was also set into the epoxy under the aerial to help protect this important part in case the turtles wedged themselves under hard substrate whilst resting during internesting at Ascension Island. The transmitters were positioned on top of the carapace to allow the aerial to be clear of the water in order to transmit to the satellite when the turtle surfaced. This makes it more liable to damage during internesting and any subsequent mating, so the rugged model originally designed for use on seals that haul out and roll on the ground, was used to hopefully prevent this.

3.1.3: Other data sets included:

In order to provide a larger sample size to compare foraging areas between different turtles, data were collated from two previous tracking studies of green turtles in the Atlantic Ocean. These data were then compared to that received from the SMRU transmitters with respect to the size of the turtles and the home range choices.

The first results were provided by a Telonics ST-10 PTT that was attached to a green turtle nesting on Long Beach, Ascension Island on the night of 1-2 June 1998 (Hays et al., 2001b). It was the first turtle for which location data had been received during both the post-nesting migration and for a period in the Brazilian coastal waters. Data were also available from turtles that had transmitters attached after being captured by fisheries along the Brazilian coastline between July 2000 and May 2001 (Godley et al., 2003). This was the first time juveniles had been tracked in this important foraging area. These turtles were released into the sea after attachment close to the area in which they had been captured. The transmitters, Telonics ST-18 PTTs, also provided location data only. Three of the seven tracked turtles were seen to cease coastal movement and maintain distinct home ranges during the study.

3.2. Data processing:

3.2.1: Location data.

3.2.1.1: Location filtering:

These transmitters provided locations via the ARGOS system (Toulouse, France), which involves three parts- transmitters, satellite-based receivers and ground data processing. When the animal is at the surface, the transmitter repeatedly sends out a signal of known frequency, which can be received only when the satellite is visible above the local horizon. Locations are computed from all the messages received during a satellite pass. The Argos system calculates locations by measuring the Doppler Effect[3] on transmission frequency (Argos, 2008). When the satellite approaches a transmitter, the frequency of the transmitted signal measured by the onboard receiver is higher than the actual transmitted frequency, and lower when it moves away. The perceived frequency of each message is measured and the possible position of the transmitter is computed. This system assigns levels of accuracy or location class (LC) to each location fix primarily depending on the number of uplinks received by the satellite during an overpass and hence how accurate it perceives the

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[3] The Doppler Effect is the change in frequency of a sound wave or electromagnetic wave that occurs when the source of vibration and observer are moving relative to each other (Argos, 2008).

location to be (Argos, 1996). There are 6 classes used: 3, 2, 1, A, 0 and B. LC 3, 2, 1 and 0 are only provided when at least 4 uplinks have been received in a single overpass, LC A when 3 uplinks have been received, and LC B when only 2 have been received. If speed of travel or home range is to be calculated, any erroneous points must be filtered out as even small inaccuracies in the location data can lead to errors in the calculations. Argos provides an indication of the accuracy of LC 3, 2, 1 and 0. Previous studies have shown that fixes of LC A are accurate enough to be used for small scale tracking studies whilst locations of LC B and 0 are too inaccurate (Hays et al., 2001b).

3.2.1.2. Home range of Atlantic turtles:

Using the locations, data were temporally divided for each turtle into 5 phases; internesting at Ascension Island, open-sea migration, approach to Brazil, coastal migration, and foraging. Data were not recorded for all individuals for each of these phases.

With the Ascension and Brazil attachments, the location data were examined to determine the areas utilised by the turtles off the Brazilian coast. The locations were filtered by speed (all fixes implying a travelling speed greater than 5 kmh^{-1} were removed) and then by rejecting the most scattered 35%, a cluster of points was apparent and this was used to describe the centre of the area selected by each turtle. Admiralty charts of the area were digitised by overlaying a grid and converting co-ordinates into latitude and longitude to provide a bathymetry map of the areas inhabited by the turtles. Plotting the calculated home range centres onto these maps allowed initial inferences to be made about the depth choices for each turtle. The possible sizes of the home ranges were determined.

3.2.1.3: Speed of travel:

An equation published in Hays et al. (2001b) states when using fixes of LCB, the minimum distance between 2 locations that is required to ensure that the calculated speed of travel lies within 10% of the true values on 95% of occasions is 87 km. The accuracy of the B class locations in that study was known from trials in fixed positions before deployment. As no such trials were applied here, the true accuracy of each location class is unknown and therefore other tests must be applied to ensure a genuine description of the travelling speed of these turtles.

First consecutive locations were used to calculate speeds of travel. The distance between each consecutive fix was calculated using a great circle equation assuming a straight-line movement between the fixes. Then the data were filtered to remove the effect of erroneous points. Any points that were obviously erroneous, leading to speeds over 5 kmh^{-1} (which is considered a biologically unrealistic speed of travel (for example, Luschi et al., 1998)) were discarded. There was still a high variability of speed and low autocorrelation between the points. The Mediterranean turtles only performed short open sea migrations (turtle 4148 only migrated 309 km) and therefore, when including LC B fixes in the analysis, it was unsuitable to use a minimum distance criteria of 87 km (Hays et al., 2001b) between consecutive points to ensure an accurate representation of the speed of travel. This was only suitable for the Ascension Island attachments where turtles migrated over 2000km. Therefore the effect of using a minimum time difference between fixes instead of distance was considered. Previous studies have set a minimum time interval between consecutive fixes used for speed calculations, for example, ranging from at least one hour between fixes (Hamer et al., 2001; Hull et al., 1997) to calculating a daily mean position (e.g. Burns et al., 1999). So, here, different time intervals were chosen to see what effect this had on the speed of travel calculations. Each fix was taken in turn and speed of travel was calculated between this fix and the next one that was between 1 and 3 hours later. Then the second fix was compared with one 1 to 3 hours after this, and so on. This was then repeated with a time interval of 3 to 6 hours, then increasing in 3 hour increments up to 21-24 hours. The results showed that an interval of 12 hours or more could be considered an accurate time interval as the correlation between points showed a good relationship (figure 3.1, p. 67). The open sea phase was used for this analysis as the coastal travelling speed may vary between fixes anyway depending on possible changes in behaviour, for example, resting or opportunistic foraging. Initial data screening removed all fixes received from around Cyprus, along the coast, those that would imply travelling speeds greater than 13 kmh^{-1} from the previous fix (Luschi et al., 1998), and any that were clearly anomalous. Then, each fix was taken in turn and speed of travel was calculated between this fix and the next one that was at least 12 hours later. Then the second fix was compared with one at least 12 hours after this and so on. In order to minimise the effects of any inaccuracy in location fixes or the effect of any erroneous results, each fix was only used once as the second location in a speed calculation.

3.2.1.4. Travelling speed and diving behaviour:

The post-nesting migration of the three Mediterranean turtles was divided up into open sea migration and coastal migration. As the data were collected in 6 hr

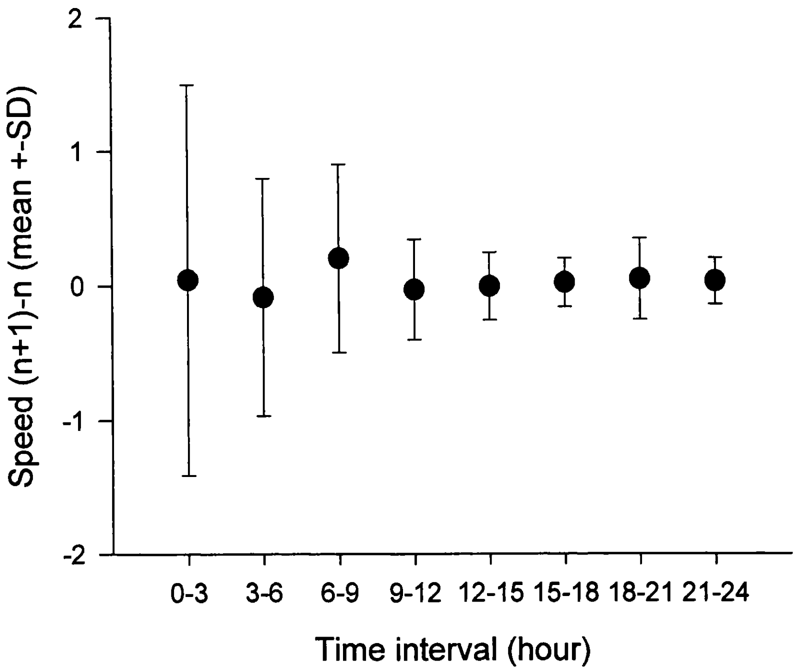


Figure 3.1: The mean difference (±S.D.) between consecutive speed calculations for varying time intervals. (See text for how speed was calculated for each 3 hour time interval). Data shown are from the open sea migration of turtle 4149. The graph shows the point at which the minimum time interval between fixes used to calculate travelling speed would have no significant effect on the autocorrelation between consecutive speed results. In this example, fixes used to calculate travelling speed should be at least 12 hours apart. After this value, a Tukey multiple comparison test shows no significant difference between the 3 hour intervals.

histograms, fixes of LC 3, 2, 1 and A were selected that allowed speed of travel to be calculated corresponding to a 6 hr period when dive data was available. This allowed the speed of travel to be compared to mean dive duration and depth, and stepwise linear regression was carried out in order to find any relationship between speed of travel and different variables of dive behaviour. Statistical analyses were performed with Minitab (Release 10.51 Xtra For Windows) and Practistat (2002).

The SRDLs attached to Ascension Island turtles did not provide a sufficient quantity or quality of location data to allow comparison of speed and diving behaviour in 6hour periods and hence data were divided into 2 day intervals for this analysis.

3.2.2: Diving data:

3.2.2.1. SDRs (Mediterranean 1998):

SDRs compress and transmit dive data in the form of histograms. The histograms summarise information on maximum dive depths and dive duration. The transmitter collects, compresses and encodes the data into these histograms, which consist of a set of bins, each of which contains counts for a given range of depth or time. The transmitter samples depth every 10 seconds and determines the maximum depth of each dive. At the end of each dive the appropriate bin is incremented. Each dive provides one count for maximum depth and one count for duration. The counts are accumulated for a 'histogram period' defined as 6 hours. Therefore, a depth histogram contains the number of dives whose maximum depth fell within that bin's range during that histogram period. A duration histogram contains the number of dives whose duration fell within that bin's range. The number of bins assigned to each type of histogram and the upper limit of these bins is user-definable. For example, the

SDRs for this study were programmed to have 10 depth bins, with the upper limit for the bins as 5 m, 10 m, 15 m, 20 m, 25 m, 30 m, 35 m, 40 m, 45 m and 234 m (which is the maximum depth recordable by these transmitters). Therefore, if the maximum depth of a dive were 22m, the fifth (25m) bin would be incremented by one. The upper limits of the dive-duration histogram bins are: 5, 10, 15, 20, 25, 30, 45, 60, 90 min and a final bin with no upper limit. The temperature data were provided as 'time-at-temperature'- the proportion of time spent at different temperature ranges with maxima of 4, 8, 12, 16, 20, 24, 28, 32 and 36°C and hence the mean temperature could be calculated using the midpoint of each bin.

At the end of a histogram period, the counts in the histograms are moved to the 'transmit buffer' and new counts are accumulated. The histograms are compressed and concatenated into a histogram message. This optimises the amount of data in each transmission. When histograms are formatted for transmission, empty bins are not used and, in addition, 2 histograms may be concatenated into one message. The transmit buffer contains histograms from the previous four histogram periods (last 24 hours), the SDR cycles through the transmit buffer, transmitting each histogram in sequence (e.g. oldest depth, oldest duration, oldest time-at-depth, next oldest depth, next oldest duration, etc.), one histogram at each transmission interval. Therefore, there can be multiple transmissions of the same histogram during the 24 hours the histogram is in the transmit buffer.

The units used in this study measured depth from 0 to 234 metres with a resolution of 1 metre. The shallowest depth considered to be a 'dive' is 2 metres. 'Dives' are defined as starting when the SDR depth sensor reads deeper than 2 m <u>and</u> the conductivity sensor reads 'wet', and ending when the depth sensor reads shallower than 2 m or the conductivity sensor reads 'dry'. The depth and conductivity sensors are measured every 10 seconds, so a surfacing shorter then 10 seconds may be missed.

The six-hour periods were set to allow coverage of (0)'night', (1) 'dawn', (2) 'day' and (3) 'dusk' behaviour patterns. The periods used for the 3 turtles in this study were the same; (local time (GMT+3h) (0) 21:00 to 2:59 (1) 3:00 to 8:59 (2) 9:00 to 14:59 (3) 15:00 to 20:59. The transmitter calculated which period (0-3) the histogram belongs to.

The total submergence time for each 6-hour period was calculated by multiplying the number of dives in each duration bin by the midpoint of the duration range of that bin. The remainder of the 6 hours was spent between the surface and 2 m as any dives shallower than this depth would not be recorded by the transmitter. In 6 h periods where dives longer than 90 min were recorded, a mean submergence could not be calculated as assuming median duration of the final bin could lead to misinterpretation of the results because dives could be anywhere from 90 min to 360 min (6 hours) in duration. Data were divided into autumn, winter and spring phases by movements seen by the turtles and a corresponding distinct change in dive behaviour (see Godley et al., 2002). Sunrise and sunset times were extracted from a program provided by GeoScience Australia (www.auslig.gov.au).

3.2.2.2. SRDLs (Ascension 2001):

SRDLs were equipped with a pressure sensor to provide depth measurements and a salt-water switch to allow the processor to detect when the transmitter was underwater. Transmissions were then prevented when the unit was underwater conserving battery power. The onboard micro-processor collected the values read by the sensors and summarised and compressed this information into messages ready to be sent. Each dive entered a buffer within the SRDL so that these data would be randomly transmitted for the next 5 days and, therefore, the specific dive profiles obtained via the Argos system were not weighted by the surfacing behaviour of the turtle immediately subsequent to each dive (Myers et al., 2006).

A submergence was considered a dive if a pressure measurement over 6m was received. Then the processor selected the 5 major inflection points of the dive (the points where the trajectory of the dive changed most rapidly) (figure 3.2, p. 72). If an inflection point occurred above 6 m during a dive it was encoded as 0 m. The salt-water switch also performed badly, missing some start and end points of dives or encoding two dives as one. This meant the data set had to be manually examined and some dives corrected to take these anomalies into account as they may affect the calculated maximum depth or duration of dives. When the end point was missed the recorded dive duration was longer than that which actually occurred (figure 3.3, p.72). The recorded duration therefore includes actual time diving (A) and a portion of time that should be recorded as shallow diving (B). If two dives were encoded as one, then the maximum depth recorded would only be for the deeper of the two dives (figure 3.4, p. 73). For any dives less than the 6 m threshold, no profile was calculated, but the unit recorded the maximum depth and duration of the dive. 6-hour summaries were also calculated that provided an indication of the amount of time spent engaged in dives greater than 6 m depth and allowed the average depth for this period to be calculated, including all dives whether above or below 6 m maximum depth. The 6

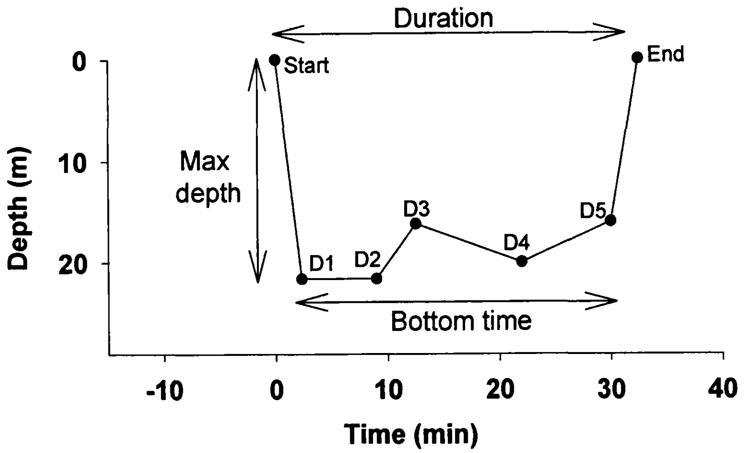


Figure 3.2: Typical dive profile produced by SRDL. D1 to 5 are the five inflection points recorded. Start to D1= descent time, D5 to end = ascent time, D1 to D5 = bottom time.

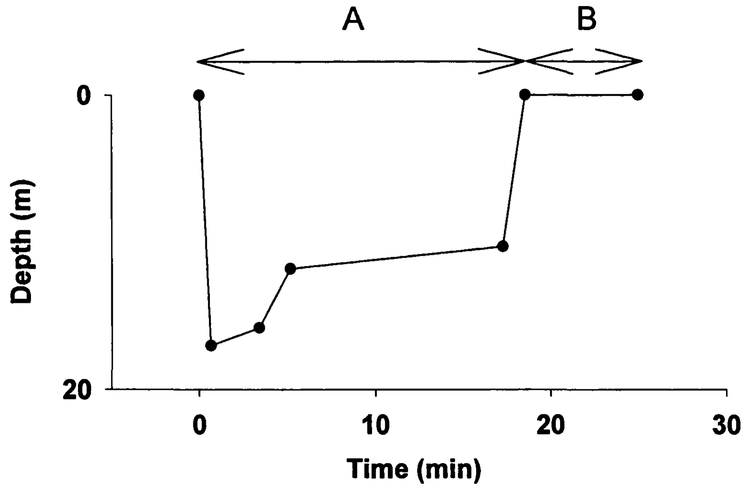


Figure 3.3: Typical midwater dive profile where the end point has been missed by the processor. The actual dive duration is **A**, but the processor records it as **A+B**. **B** is probably a period of shallow diving.

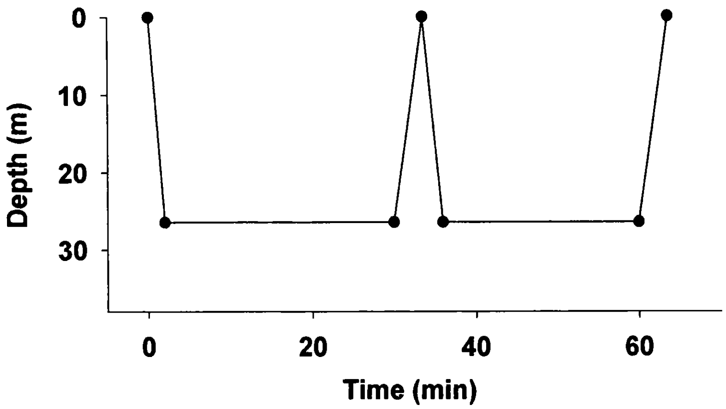


Figure 3.4: A profile taken from the record of 21914 that could be an example of two U-dives that have been encoded as one dive as the surface interval in between has been missed by the processor.

hour summaries record information for night (0), dawn (1), day (2) and dusk (3); (local time (GMT - 3 h) (0) 21:00 to 2:59 (1) 3:00 to 8:59 (2) 9:00 to 14:59 (3) 15:00 to 20:59.)

The dive data were divided into phases of migration using the locations provided by Argos in order to separate the information received when the turtles had ceased movement and became resident in coastal waters off Brazil. Data were received for 4 turtles after the migration had ceased. Statistical analyses were carried out using Minitab and Excel.

3.2.2.3. Note on 'bottom time' and 'time within 2 m of the maximum depth':

If continuously recording time-depth recorders are used during a diving study, then an accurate description of the bottom time of a dive can be obtained so that it can be seen if the proportion of this during a dive varies depending on dive type and function.

In this study, the time spent within 2 m of the maximum depth was calculated to represent the bottom phase of a dive (cf. Hays et al., 2000a; Martin, 2003). Normally, bottom time of a U-dive would be simply T5-T1 but, because the 'bottom phase' of a dive may not be a true indication of time spent at depth due to depth variations during submergence or an inflection point recorded as the turtle descends or ascends, this could lead to incorrect calculations (Figure 3.5, p. 75). The calculation would not select the correct bottom time but would include the portion of time until the last inflection point before surfacing. Therefore, I created a calculation to calculate the percentage of time during the dive that was within 2 m of the maximum depth of the

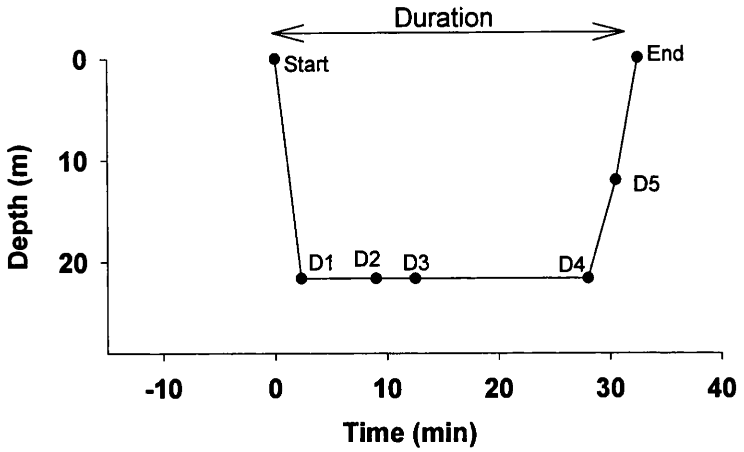


Figure 3.5: An example of a U-shaped dive with an inflection point recorded during the ascent phase. If bottom time was automatically calculated as the proportion of dive time between D1 and D5, then this would be incorrect as the time between D4 and D5 should be included in the ascent time. The bottom time should be the time between D1 and D4.

dive. This also allows variations over 2 m in the bottom phase to be picked up, so separating flat-bottomed dives. The example in figure 3.6 (p. 77) shows the portion of the dive that is within 2 m of the maximum depth. The percentage of each dive duration that is spent within 2 m of the maximum dive depth was calculated for each dive profile (figure 3.7, p. 77).

3.2.2.4. Swim-speed data:

Swim-speed data were provided by the SRDLs as 3 values for each profile, calculated as speed during the descent, bottom and ascent phases. The values were provided in m/s. The sensor calculates the swim-speed of the turtle by measuring the rotation of an internal paddle wheel. The three values calculated by the microprocessor were descent speed (start of the dive to D1), bottom speed (D1 to D5) and ascent speed (D5 to dive end). The distance of each phase was calculated by multiplying the speed by the duration of that phase and then the overall mean speed for the dive equalled the sum of these distances divided by the total dive duration. The swim-speed sensor was positioned on top of the SRDL and hence was the most susceptible part of the equipment to damage during internesting. When turtles were observed re-nesting, it could be seen in many cases that the sensor was broken away or badly damaged. By comparing the speed data and the vertical distance travelled, it was apparent that the swim-speeds were underestimated, perhaps due to damage or clogging of the sensor. Therefore the swim-speed data was examined qualitatively to compare between dive types.

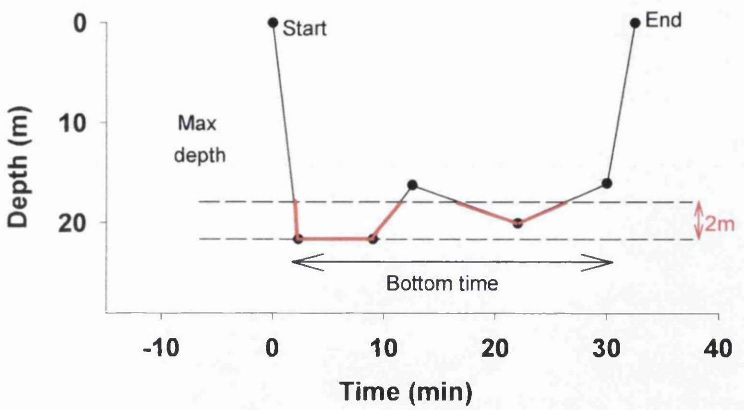


Figure 3.6: Typical dive profile. Red sections highlight the time within 2 m of the maximum depth.

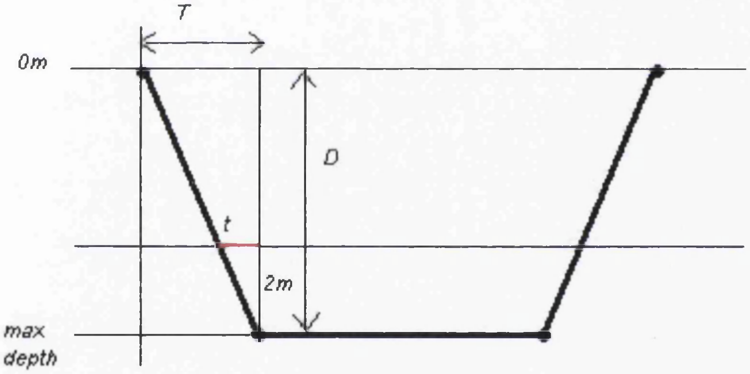


Figure 3.7: The first portion of 'bottom time' (time within 2 m of the maximum dive depth) at the end of the ascent phase can be calculated as both 'T' and 'D' are known variables. 't' can be calculated because:

$$\frac{D}{T} = \frac{2m}{t}$$

If the next inflection point is within 2 m of max depth then the whole of the time between is incorporated, if not then the portion of time can be calculated as above, and so on. If the inflection point is not the maximum depth, the difference between this point and the max depth can be subtracted from 2 m.

CHAPTER 4

Location Data; Migration Routes, Swimming Speed and Home Range

4. Location data; migration routes, swimming speed and home range.

4.1. Performance of satellite transmitters:

4.1.1. Deployments in the Mediterranean Sea:

In this thesis data are examined that were received from satellite-linked transmitters attached to 3 nesting green turtles in the Mediterranean Sea. The routes undertaken by these turtles are seen in figure 4.1 (p. 80). These transmitters provided data for the longest period of time of all the deployments examined here; during post-nesting migration, then after arrival at the foraging grounds, throughout the subsequent winter and into the next spring (table 4.1, p. 81).

4.1.2. Deployments in the Atlantic Ocean:

In 1998, a single transmitter provided location data for a turtle migrating from Ascension Island to Brazil showing clearly an open sea migration, followed by a coastal phase and then a period of restricted movement close to the coast of Brazil (4394B) (used as a case study in Hays et al. (2001b)). In 2001, seven more attachments were made to nesting green turtles with varying success. Details of the deployments at Ascension Island are given in table 4.2 (p. 82). All turtles migrated west from Ascension Island and of the 8 deployments, 5 were followed throughout the entire post-nesting migration until they ceased movement along the Brazilian coastline (figure 4.2, p. 83). The transmitters provided location and diving behaviour for 4 turtles throughout open sea, subsequent coastal migration and for a period of time once migration ceased (15119, 15122, 21914, 4394A). For another turtle, data were received during the open sea phase but the transmissions stopped during coastal

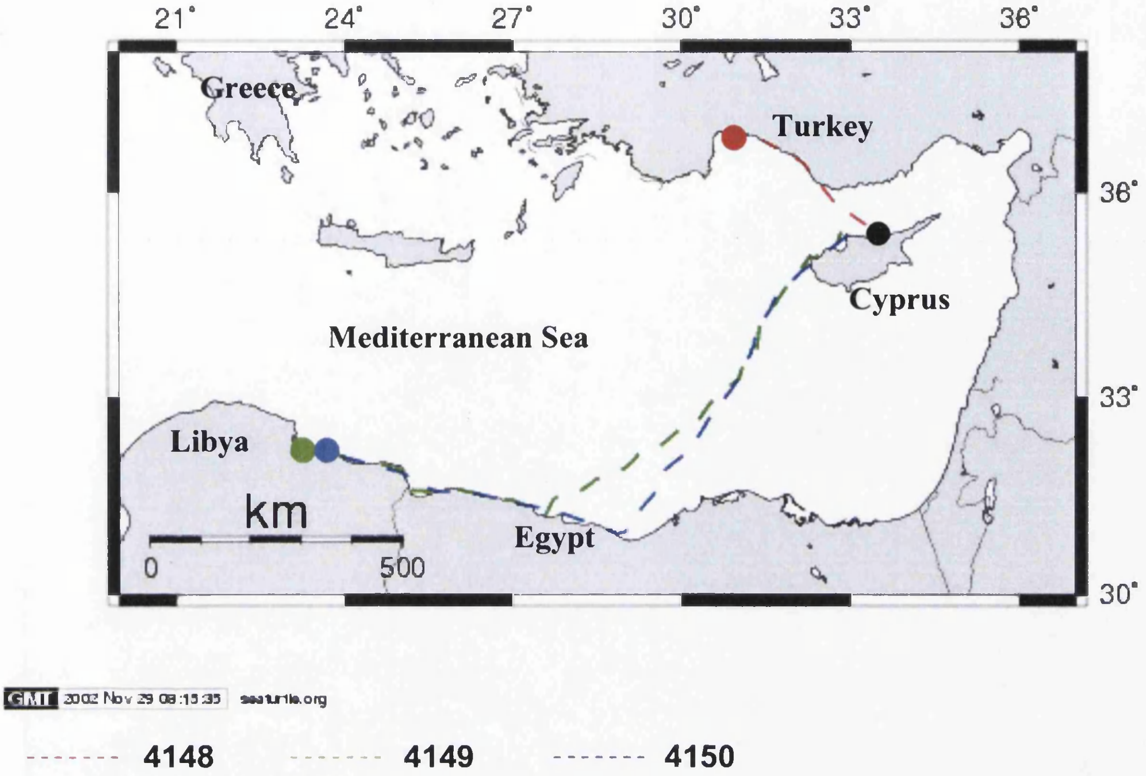


Figure 4.1: Post-nesting migration of turtles as recorded by satellite-linked recorders attached between July 28 and August 1 1998 on Alagadi Beach, Northern Cyprus (●). Circles indicate residence areas.

Individual	Start	No. Days	Locations							Dive information			
										Depth		Duration	
			3	2	1	0	A	B	Total	Histograms	Dives	Histograms	Dives
4148	1 Aug 98	289	18	19	33	26	103	213	412	316	8371	329	8972
4149	30 July 98	221	12	32	32	30	115	194	415	272	14586	263	12153
4150	28 July 98	293	30	50	44	39	156	267	586	384	17877	362	16796

Table 4.1. Performance of satellite transmitters on Mediterranean green turtles. For each individual, the date of deployment, longevity of transmissions, the number of ARGOS locations received per location class (LC) and the amount of dive information provided presented as the number of 6hour histograms and actual number of dives these contained.

PTT	CCL	Attachment date	Renested?	Leaves Ascension	Last data received	No of days	Migration phases recorded
15119	118	24/05/01	07-08/06/01	13/06/2001	27/09/2001	126	A, S, C, B
15120	112	29/05/01	11/06/01 am	14/06/2001	07/10/2001	131	A, S, some C
15121	104	28/05/01	X	29/05/2001	25/07/2001	58	A, S, some C
15122	113	29/05/01	12/06/01 am	12/06/2001	30/10/2001	154	A, S, B
21914	101	09/07/01	X	10/07/2001	30/10/2001	113	A, S, C, B
4394A	117	30/05/01	??	30/05/2001??	24/08/2001	86	Some S, C, B
4395	114	26/05/01	07/06 and 30/06??	??	20/07/2001	55	A, some S
4394B	117	02/06/98	X	04/06/1998	21/08/1998	80	A, S, C, B

Table 4.2: Attachment dates, turtle size (measured as curved carapace length (CCL)) and longevity of results for Ascension deployments. '??' indicates estimated or unknown values due to paucity of data. The migration phases are indicated as follows: A-Ascension Island, S-open sea migration, C-coastal migration and B-in Brazilian waters once movement has ceased.

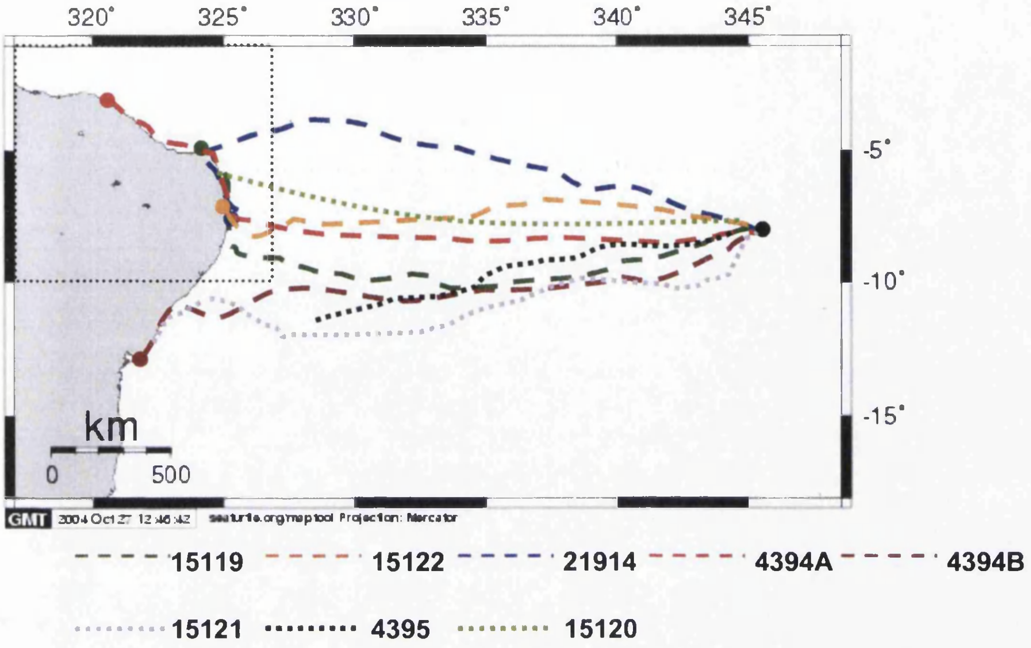


Figure 4.2: Post-nesting migration of turtles as recorded by satellite-relay data loggers attached in 1998 (n=1; 4394B) and 2001 (n=7) on Long Beach, Ascension Island (•) where transmissions continued to foraging grounds. Circles indicate residence areas (transmissions ceased before residence area was established for individuals 15121, 4395 and 15120.) (Inset shows area included in figure 4.3, p. 85)

migration before the turtle had ceased movement (15121). (The routes from the Ascension attachment that include both open ocean and coastal migration are described in Hays et al. (2002), where individuals A-E equate to PTT numbers 15119, 15121, 15122, 21914 and 4394A respectively.) The remaining two SRDLs (15120 and 4395) ceased transmissions during oceanic migration providing only a limited data set.

The movements seen by 3 individuals released off the coast of Brazil after incidental capture in fisheries are shown in figure 4.3 (p. 85) (see Godley et al. (2002) for more detailed maps). Individuals 21872 and 21874 remained close to the area of release which is approximately 50 km from where 4394A ceased migration. Individual 23709 travelled approximately 670 km southeast along the coastline passing the areas chosen by 15119 and 4394A before ceasing movements.

The quality and quantity of data received varied greatly between the individuals (table 4.3, p. 86). The number of locations per day ranged from 0.3 to 3.4 (mean = 1.56, n = 11 individuals) though the majority of locations received for all individuals were of the lower accuracy classes (B, A and 0) (mean 92%, n=11 individuals). There was great variation in the amount of dive information transmitted by each SRDL but overall 434 6 h summaries and 3094 individual dives were recorded, 2005 of which were dive profiles.

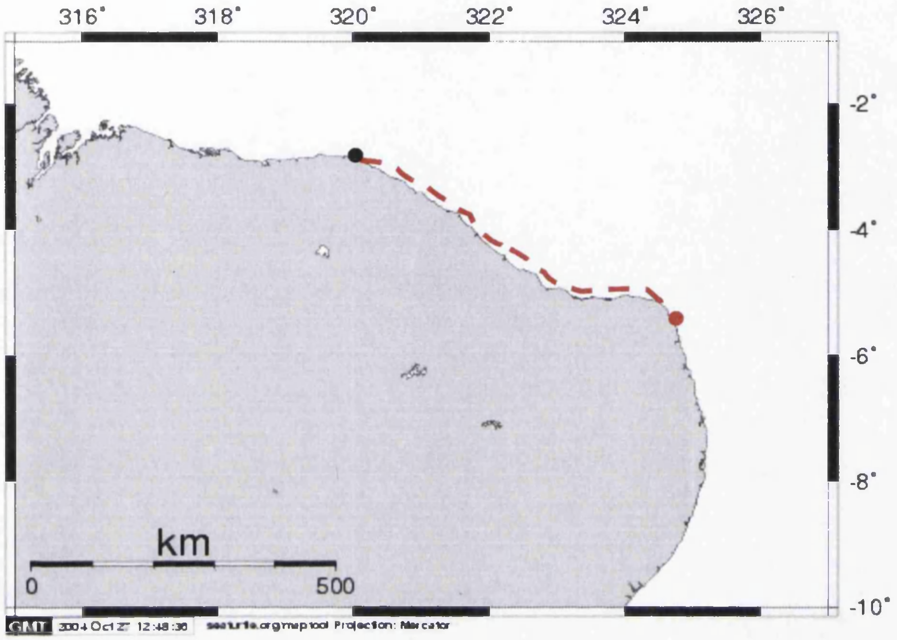


Figure 4.3: Migration of 23709 after release from Almofala, Brazil (●) as recorded by a satellite transmitter attached in 2001. The red circle (●) indicates the residence area. Individuals 21872 and 21874 released in 2000 remained in the vicinity of the release site (●) for the duration of the tracking study.

PTT	Duration of transmissions (d)	No. of locations in each class							Amount of dive information (n)		
		3	2	1	0	A	B	Total	Summaries	Profiles	Shallow
15119	126	0	2	10	24	53	181	270	106	503	365
15120	131	1	2	2	1	5	32	43	20	125	24
15121	58	0	2	10	3	10	29	54	26	119	92
15122	154	1	8	16	22	86	158	291	138	570	364
21914	113	1	2	16	30	37	116	202	106	390	170
4394A	86	0	0	1	2	7	21	31	16	67	19
4395	55	2	0	1	2	12	25	42	22	132	19
4394B	80	2	5	18	19	74	154	272	-	-	-
23709	54	0	2	2	5	27	71	107	-	-	-
21872	96	0	1	2	0	23	173	199	-	-	-
21874	197	1	2	6	0	20	275	304	-	-	-

Table 4.3: Amount of location data and dive information provided by the transmitters attached to turtles at Ascension Island and Brazil.

For 3 individuals (15122, 21914 and 4394B), a significant difference is seen between the number of locations received per day in the different phases of migration (ANOVA: 15122 $F_{3,96}$=18.09 $p<0.05$; 21914 $F_{2,107}$=20.22 $p<0.05$; 4394B $F_{2,83}$=20.67 $p<0.05$) with a post-hoc Tukey test demonstrating that a significantly higher number of locations are received per day during the oceanic phase than at the foraging grounds (figure 4.4, p. 88). For individual 15122 there were significantly more locations received during the oceanic phase than during any other, whilst with 21914 and 4394B there were significantly more locations during the oceanic phase than the foraging phase, but not compared to the coastal migration. The number of locations received during the coastal and foraging phases are significantly different for 21914 but not for 4394B (t-test: 21914 T_{22}=3.03, $p<0.01$; 4394B T_8=1.41, $p>0.05$). For the individuals for which data were obtained for both Ascension Island and foraging areas, there is a significant difference between the number of fixes per day in the two areas for individual 15122 but not for 15119 (t-test; 15122 T_{17}=2.46, $p<0.05$; 15119 T_{33}=0.29, $p>0.05$).

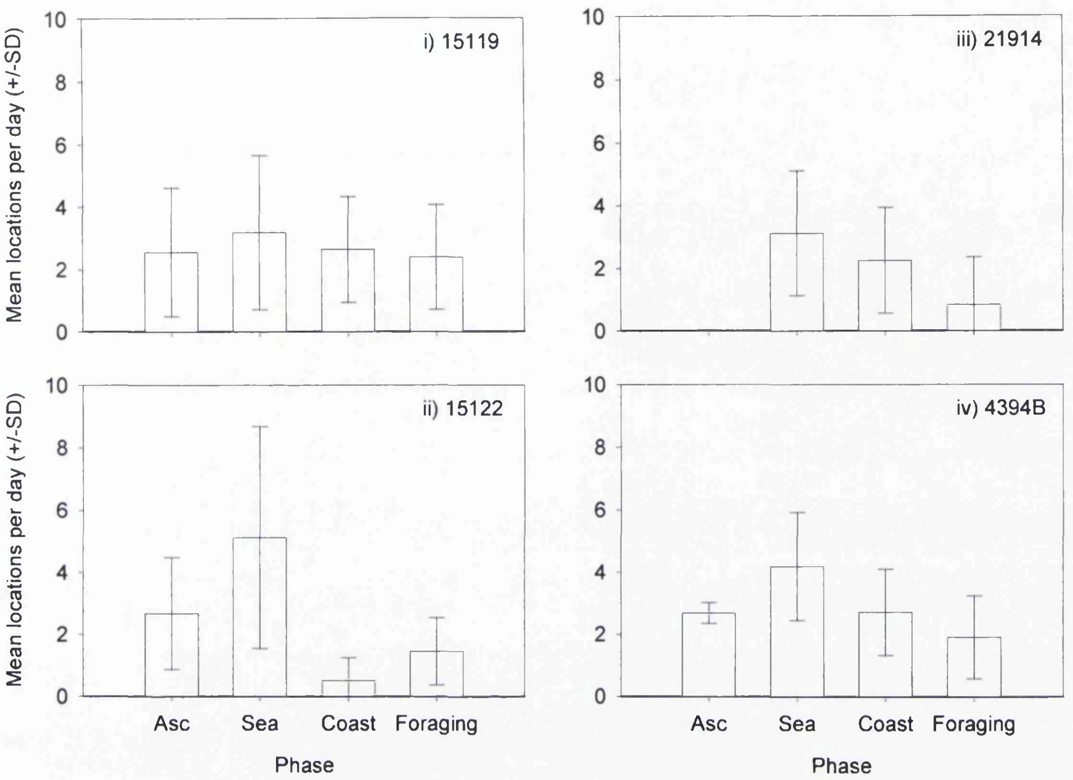


Figure 4.4: The mean number of locations received per day (+/- SD) for each phase of the migration for 4 turtles i) 15119, ii) 15122, iii) 21914 and iv) 4394B.

4.2. Speed of travel:

The distance of the different phases of post-nesting migration for the Ascension turtles was calculated as in Hays et al. (2002a), where the journey was split into 4 to 6 straight-line segments, each of which were several hundreds of kilometres long, and then the distance of each of these was added to give a total distance. This helps to alleviate problems associated with location error, which may lead to overestimation of the true distance (Hays et al., 2001b). The mean speed was then calculated from these values (table 4.4, p.90). The mean speed during oceanic or coastal migration did not show a correlation to turtle size (CCL; regression, $p>0.05$, $n=7$ individuals). The decrease in the speed of travel during the coastal phase compared to during the open sea migration mirrored with that seen for the Mediterranean turtles (open sea migration 2.7, 3.2 and 3.1 kmh^{-1}, coastal migration 1.4, 1.6 and 1.7 kmh^{-1} for individuals 4148, 4149 and 4150 respectively.) (For more detailed statistics see Godley et al., 2002.)

Sufficient higher accuracy fixes were received (LC3, 2, 1 and A) from the Mediterranean turtles to calculate speed of travel for the different stages of the route assuming straight-line movements between successive fixes. As the majority of locations for all individuals tracked from Ascension Island were of the lower accuracy classes (0, A and B), overall mean speed could be calculated using the method in Hays et al. (2002a), but in order to identify any changing trends during migration, a filtering process was employed. In order to determine the speed of travel during the oceanic phase, the locations were filtered by removing fixes that would lead to a travelling speed greater than 5 kmh^{-1} and then selecting fixes at least 90 km apart (as

ID	**CCL (cm)**	**Sea (km)**	**Sea (days)**	**Coast (km)**	**Coast (days)**	**Mean speed (km/h)**	
						Sea	**Coast**
15119	118	2309	34	396	12	2.83	1.38
15121	104	2496	43	299	15	2.42	0.83
15122	113	2277	44	57	4	2.16	0.59
21914	101	2493	35	395	17	2.97	0.97
4394	117	2233	33	792	31	2.82	1.06
4394B	117	2510	37	254	9	2.83	1.17
23709	92	-	-	670	23	-	1.21

Table 4.4: For each individual, the curved carapace length (CCL), migration length and duration and the mean speed of travel calculated from the overall distances travelled during each phase.

in Hays et al., 2001b). The autocorrelation between fixes increased greatly after the filtering process (figure 4.5 A-E, pp. 92-97) allowing the ranges of speed to be determined. The speed of travel during migration was then plotted against longitude to allow comparison between individuals (figure 4.6, p. 98). For all turtles where an open ocean and coastal phase occurred, a clear difference in speed could be seen. The range of speeds during oceanic migration varied from 1.38 to 4.12 kmh^{-1}. The general pattern of speed during the migration differed between individuals, some showing a smaller preferred range of speeds than others; 15119 showed a slight variation in speed and then it became constant, 15121 showed a general drop of speed throughout, the speed of travel for 15122, 21914 and 4394B fluctuated up and down during the migration though 21914 showed a steady drop for the second half, whilst the speed of 4394B increased towards the end.

When examining the coastal section, the method for describing temporal speed patterns by using only fixes over 90 km apart is not suitable as some turtles undertake only a short migration in shallow waters before ceasing migration. Also the number of fixes received in the coastal region is low and inaccurate. Out of 117 fixes provided for 6 individuals, only 3 were not of location class 0, A or B. The mean number of fixes per day was only 1.33 during coastal travel compared to an average of 5.48 during the oceanic migration. By incorporating diving behaviour into the location data, an estimation of speed can be determined with more confidence than by simply using the fixes calculated by Argos. Fixes calculated by Argos are known to have a level of inaccuracy that has been quantified using locations received from a fixed position (e.g. Hays et al., 2001b). The longitudinal error is seen to be significantly greater than latitudinal error. When the coastal routes for these turtles are plotted

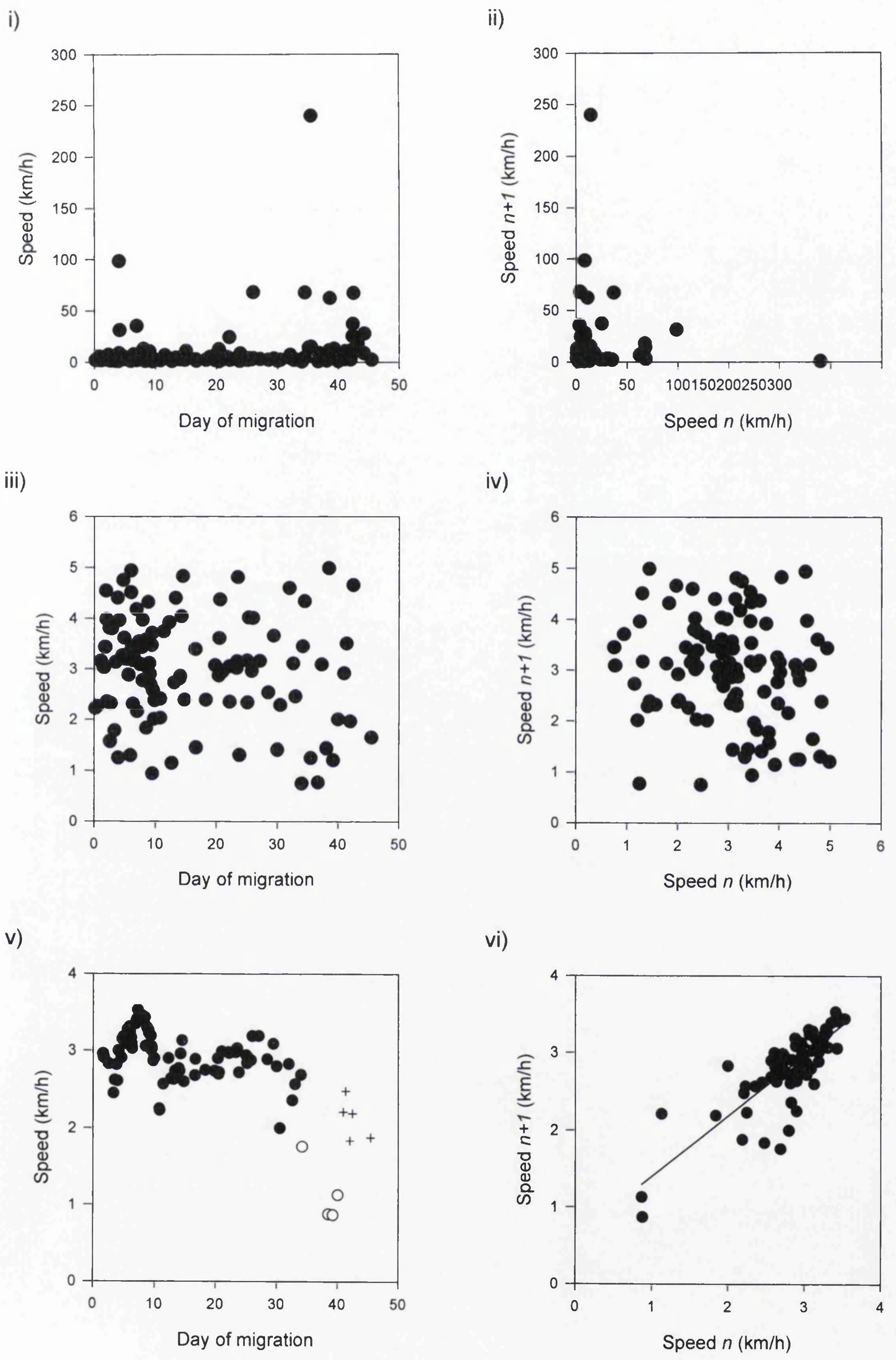

i) ii) iii) iv) v) vi)

Figure 4.5 A:15119

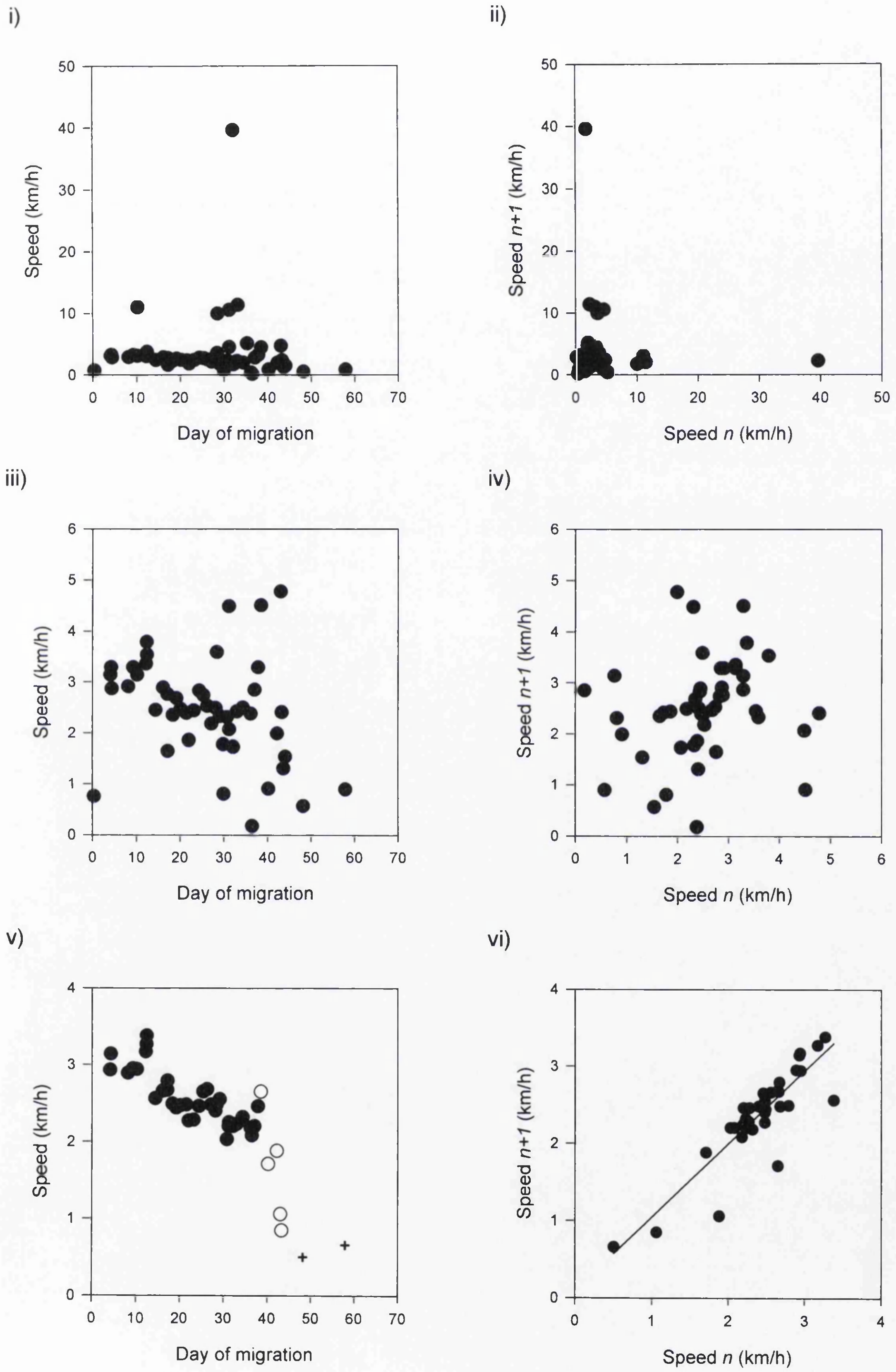


Figure 4.5 B: 15121

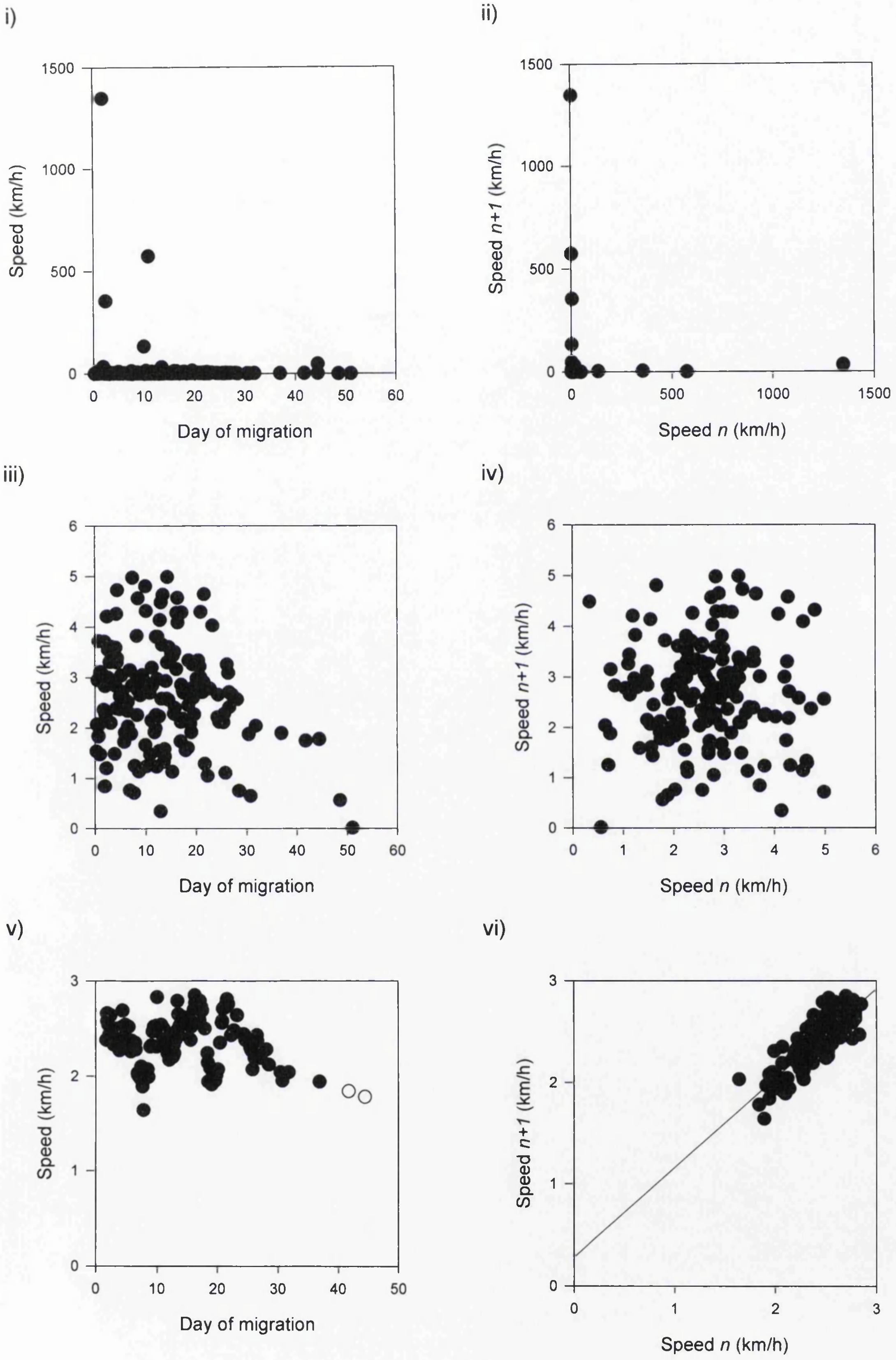


Figure 4.5 C: 15122

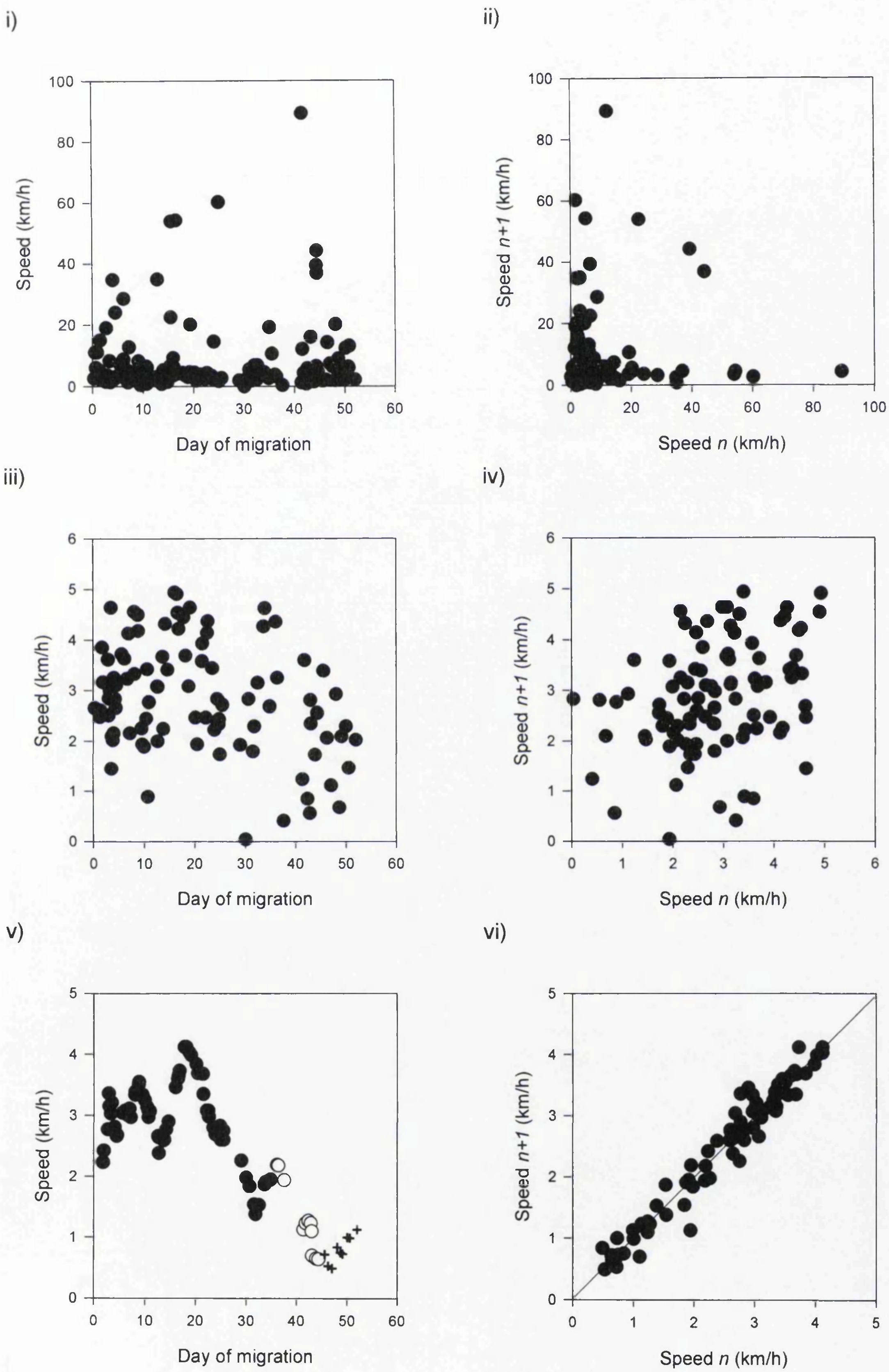


Figure 4.5 D: 21914

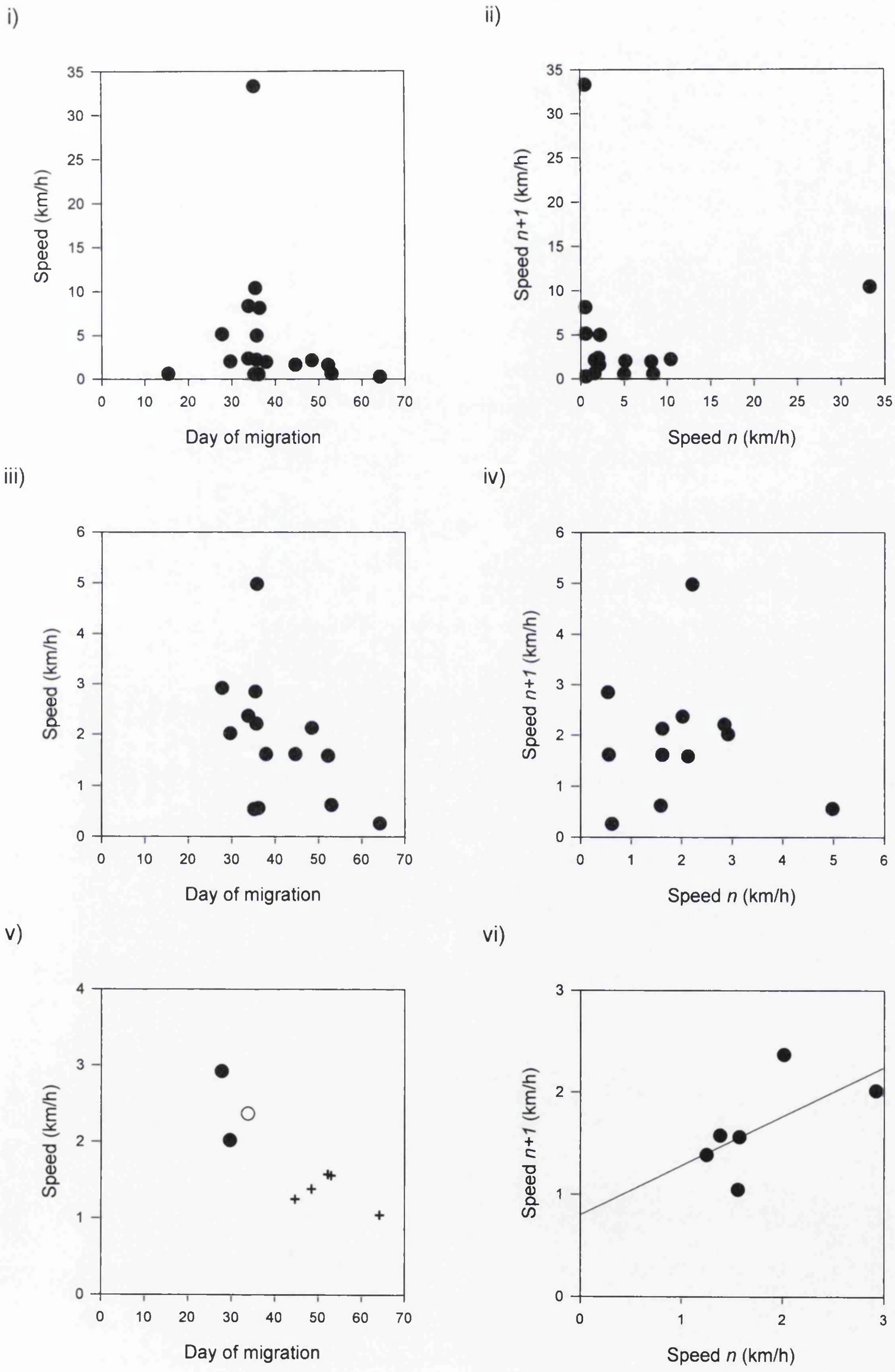


Figure 4.5 E: 4394A

Figure 4.5 A-E: Effects of filtering processes on the perceived speed of travel and the autocorrelation between consecutive speed calculations. For each individual; (i - ii) all the fixes; (iii - iv) fixes leading to speeds over 5 kmh^{-1} removed; and (v - vi) all fixes used for speed calculations which are over 90 km apart. For A(vi), $F_{1,83}=182.18$, $r^2=0.69$, $p<0.001$; for B(vi): $F_{1,36}=119.41$, $r^2=0.77$, $p<0.001$; for C(vi), $F_{1,140}=409.678$, $r^2=0.74$, $p<0.001$; for D(vi), $F_{1,79}=1597.93$, $r^2=0.95$, $p<0.001$; and for E(vi), $F_{1,4}=2.64$, $r^2=0.40$, $p=0.179$. ●: both locations are during the open sea phase, ○: one is during oceanic migration and the other in coastal waters, and +: both are during coastal migration.

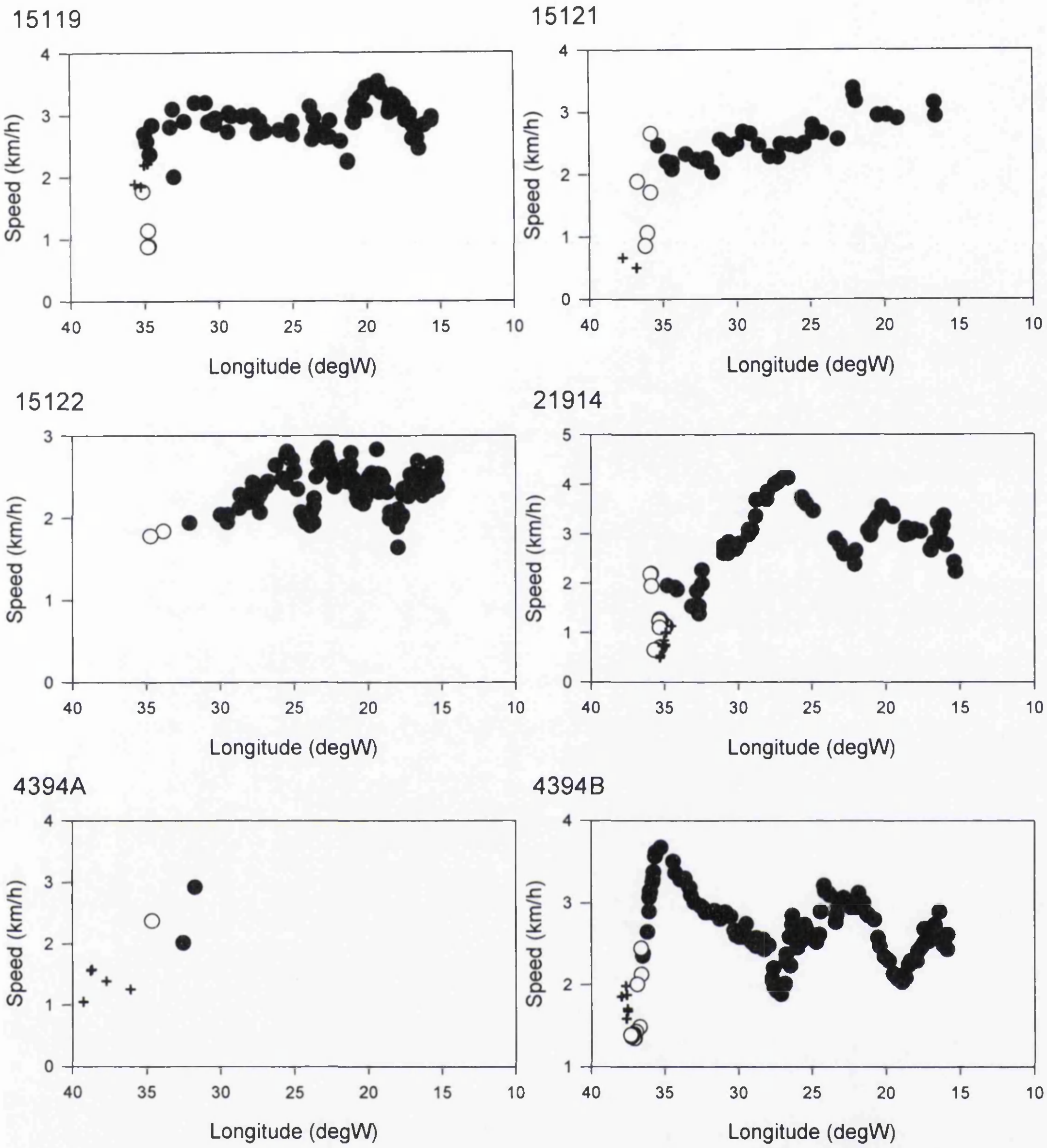
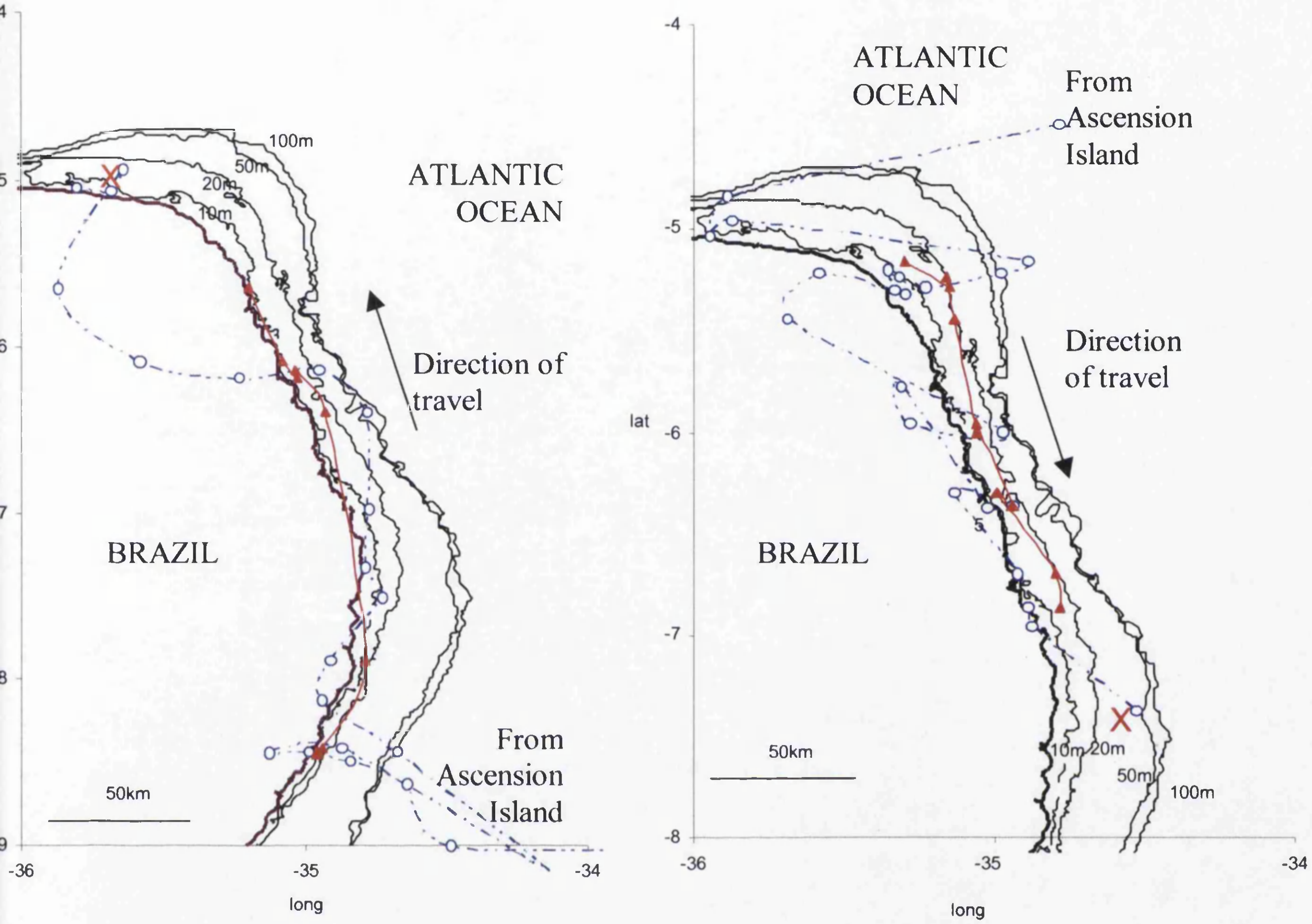


Figure 4.6: The speed of travel for the oceanic migration from Ascension Island to Brazil and any subsequent coastal travel calculated using fixes over 90 km apart; where, •: both locations are during the open sea phase, ○: one is during oceanic migration and the other in coastal waters, and +: both are during coastal migration.

(even after location filtering), the location inaccuracy is apparent due to the position inshore of some of the calculated positions and the 'zigzagging' routes produced. The turtles are seen to engage in U-shaped dives to the seafloor during coastal migration (see later section on dive behaviour) and the depths of these dives can be used as an indication of the sea floor depth at the turtle's location. If the latitude value is retained, the longitudinal value can be altered to reflect the dive depth, calculated by using the mean of the 2 corresponding depth contours at that latitude. Then speed of travel can be calculated by using the new coordinates.

This method can be applied to 2 turtles that migrate along a north-south section of coastline (figure 4.7, p. 100). When considering the speed of travel using consecutive fixes, this filtering process reduces the variation in speeds during the coastal phase (21914: original fixes, mean±SD 2.13±1.12km/h, range 0.41-4.4; altered, 1.17±0.77km/h, range 0.27-2.27. 15119: original fixes, mean±SD 2.86±1.33km/h, range 0.75-4.99; altered, 1.16±1.01, range 0.20-3.14). The turtles are seen to remain close to the coast line, 21914 mainly within 15 km of the coast, 15119 consistently within 10 km, both following a relatively similar course running between the coast and the 20 m depth contour.

Although the amount of data received is not sufficient to carry out this analysis on the other individuals, the U-dive depths for individuals 15121 and 15122 are comparable to those seen for 15119 and 21914, with the majority of dives to less than 20 m. An exception is seen with individual 4394B where 7 U-dives recorded during the first week of coastal migration are over 30 m in depth, implying the coastal migration is


A) 15119

B) 21914

Figure 4.7: The effect of changing the longitude co-ordinate to correspond with diving depth during the coastal migration phase for 2 individuals A) 15119 and B) 21914. Blue dashed lines indicate the route using the fixes provided by Argos, whilst the red line shows the route using the alternative co-ordinates. The red cross indicates the approximate position of the area where migration ceased. The thick black line indicates the coastline and the 10, 20, 50 and 100m isobaths are also shown. (Not all longitude values can be altered using this method due to paucity in the dive data, hence incomplete sections of the red line.)

initially carried out further offshore. The data set is very small considering this turtle travelled nearly 800 km after reaching Brazil but 2 more U-dives were received later during this migration phase which are both less than 15 m in depth.

4.3. Foraging areas and home range:

4.3.1. Foraging areas:

The quantity and quality of the location data provided by Argos for the different transmitters from the foraging areas varied (see table 4.5, p.102) although a high percentage of locations received for all turtles were of the lower accuracy classes (A, B and 0) (mean proportion for all turtles 0.93, SD 0.08, range 0.78-1).

When plotting the fixes and describing the home range, the clearest results with the Mediterranean attachments were seen when selecting only locations of the most accurate classes, 1, 2 and 3 (see chapter 2). This showed distinct home ranges and definable movements between the seasons. But for the turtles tracked from Ascension Island, simply filtering by location class is not realistic as the majority of fixes (>93%) were of the lower accuracy classes (0, A and B). In fact only 21 fixes of LC1, 2 and 3 were received in total from all 8 transmitters off the Brazilian coast compared to 218 from the 3 in the Mediterranean. Including fixes of the lower confidence indices could increase the number of outliers included in the analysis which could greatly affect home range sizes. A good example is seen with turtle 4394A for which only a small number of fixes were received from the foraging area (figure 4.8, p.103). By removing a few obvious outliers the mean position changes by 20 km.

Attachment	I.D.	No of days	Total no of fixes	Fixes per day (mean±SD)	Range	Location class 3	2	1	0	A	B
Brazil 2000 & 2001	**23709**	30	37	1.2±1.82	0-7	0	1	0	1	6	29
	21874	96	199	n/a	n/a	0	1	2	0	23	173
	21872	197	304	n/a	n/a	1	2	6	0	20	275
Ascension 2001	**15119**	32	79	2.4±1.68	0-6	0	0	3	0	11	65
	15122	40	58	1.4±1.08	0-4	0	0	0	1	15	42
	21914	58	49	0.8±1.56	0-6	0	0	3	10	10	26
	4394A	20	12	0.5±0.93	0-5	0	0	0	2	3	7
Ascension 1998	**4394B**	33	65	1.9±1.33	0-5	1	0	1	1	16	46
Cyprus 1998	**4148**	282	266	1.3±1.82	0-7	16	18	28	22	100	102
	4149	200	302	1.5±1.92	0-7	7	20	22	22	85	146
	4150	270	496	1.8±2.26	0-8	23	46	38	33	130	226

Table 4.5: Quantity of location data received from residence areas for all attachments included in this study. N.B. For individual 21914, there was a distinct change in the performance of the transmitter during this phase; for the first 15 days at the residence area the mean number of fixes per day (±SD) was 3.1±1.67 (range 0-6), and then for the remainder of the study it dropped to 0.1±0.29 (range 0-1).

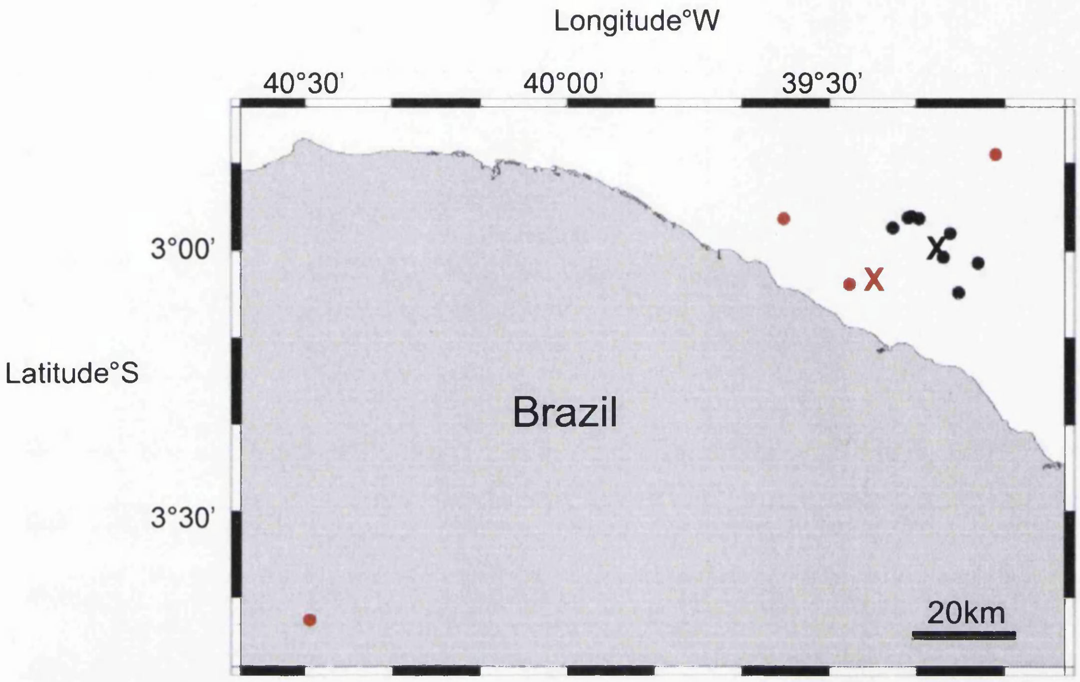


Figure 4.8: The effects of outliers on the perceived habitat of individual 4394A. Fixes in black (●) are the closest cluster, whilst those in red (●) are four outliers. The red cross (**X**) indicates the mean position calculated using all the fixes from Argos, whilst the black cross (**X**) indicates the mean position using only the closest 65% (●) for the analysis.

Previous studies have found that by removing 35% of the outlying fixes, a clear cluster of points becomes apparent, thus identifying the centre of the home range (e.g. figure 4.9, p. 105).

When calculating the size of the area of habitat use, Jiguet and Villarubias (2004) showed removing outliers will reflect a core area with a quantifiable size. By isolating outliers, a cluster can be found. The percentage of fixes to consider as outliers could be calculated by eye but a non-biased automated method was also used. The standard deviation of the straight-line distances of the fixes from the mean position was calculated. Then in turn, the furthest distance from the mean position was removed and the mean and the standard deviation recalculated. By plotting the standard deviation against the percentage fixes removed, the point at which the graph levels out indicates the percentage of fixes to remove to leave the fixes that show a clear cluster (figure 4.10, pp. 106-108). If a line is drawn from the right hand side of the x-axis along the initial linear ascent as 'fixes removed' decreases from 100% (on the graphs in figure 4.10, pp. 106-108), the percentage at which the plot curves steeply upward away from the straight line is the point where the fixes become more scattered and have a greater effect on the size of the habitat. So removal of this indicated percentage of fixes means the centre of the home range can be calculated without including effects from outliers.

As more fixes are removed, the line begins to level out. At the point where the gradient ceases to change between the fixes, it can be assumed that all the outliers are removed and the remaining fixes will be a 'cluster' and provide an indication of the core area of habitat use from which the centre of the home range can be calculated.

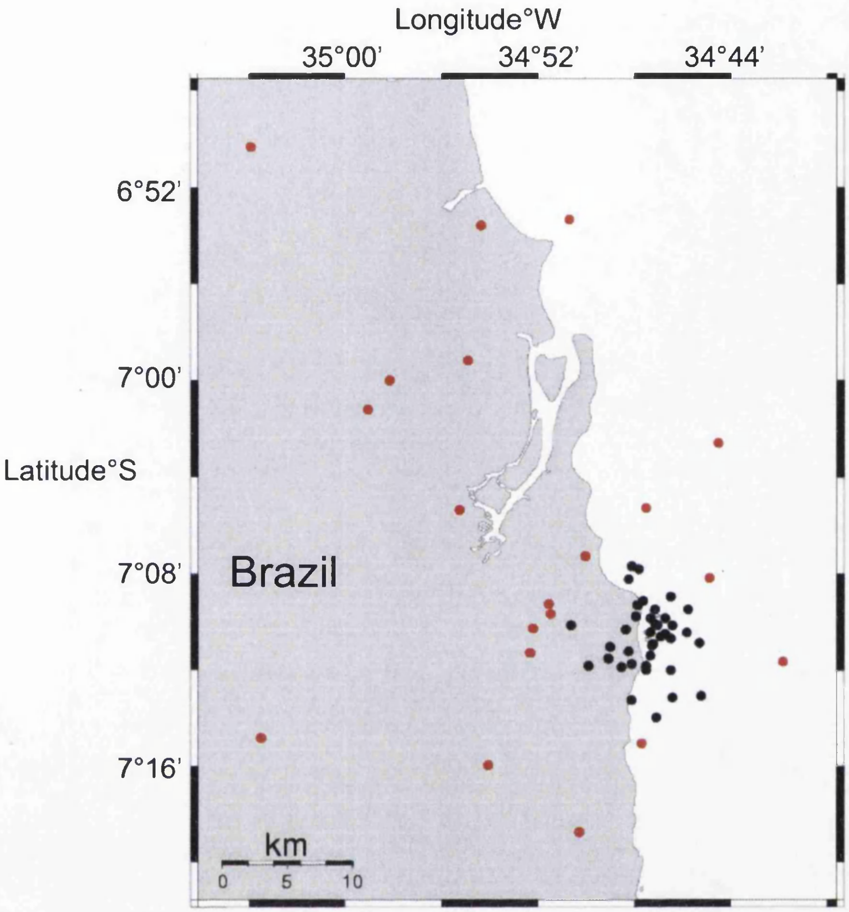
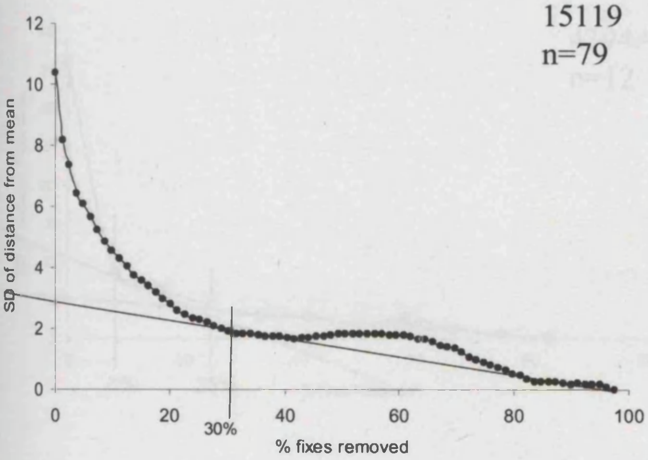
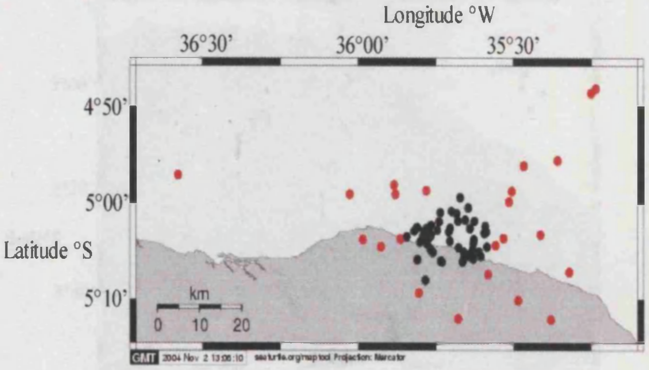
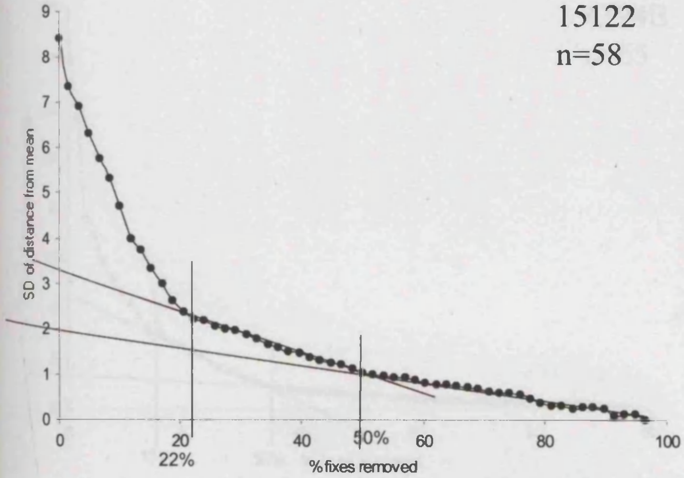


Figure 4.9: Map showing the distribution of Argos fixes for turtle 15122. Fixes in black are the closest 65%, whilst those in red would be discarded as outliers.

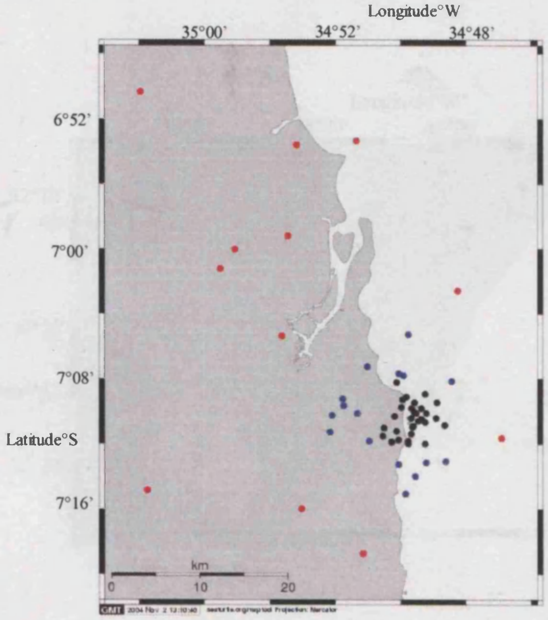


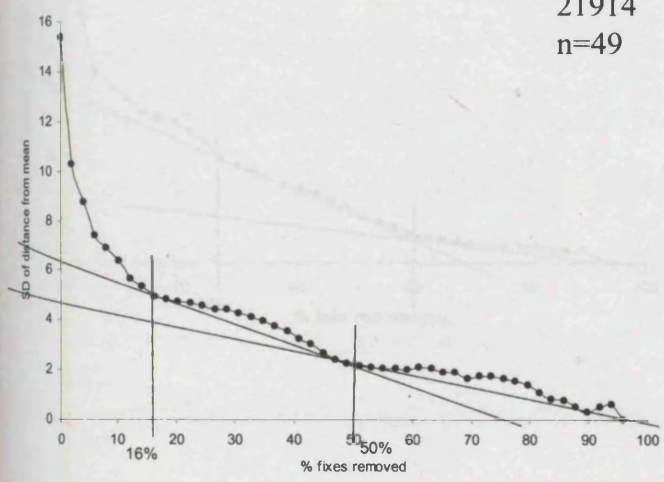
15119
n=79



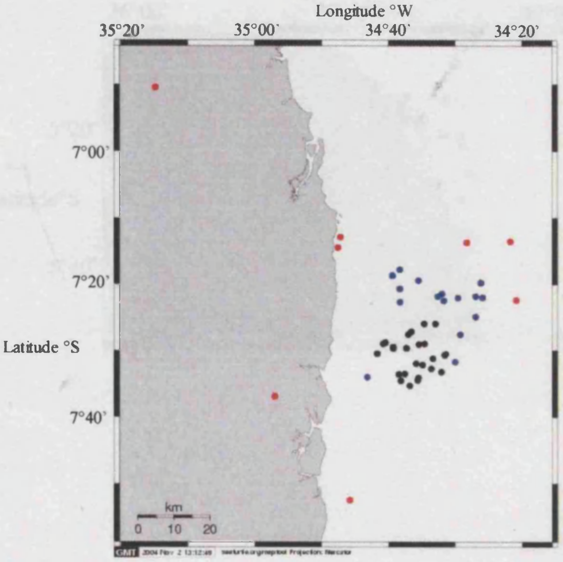


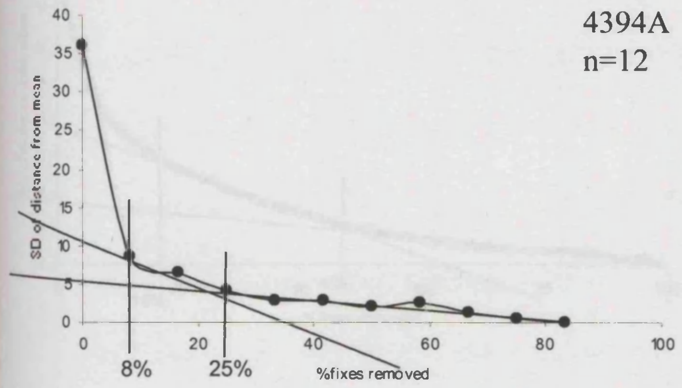
15122
n=58



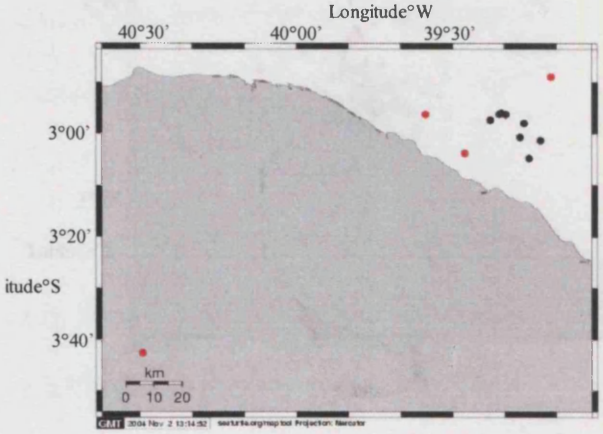


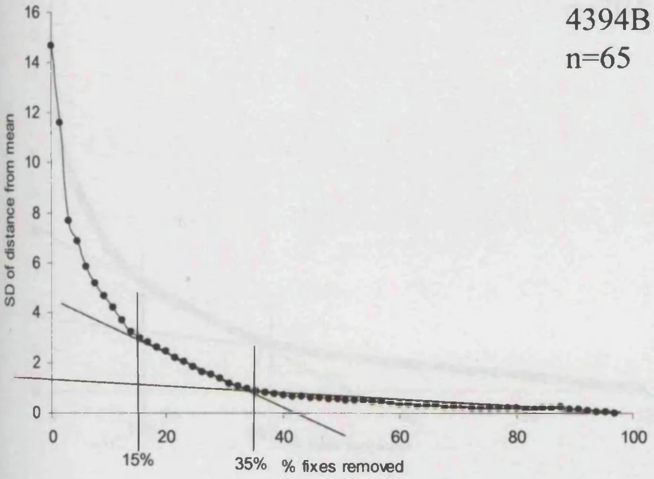
21914
n=49



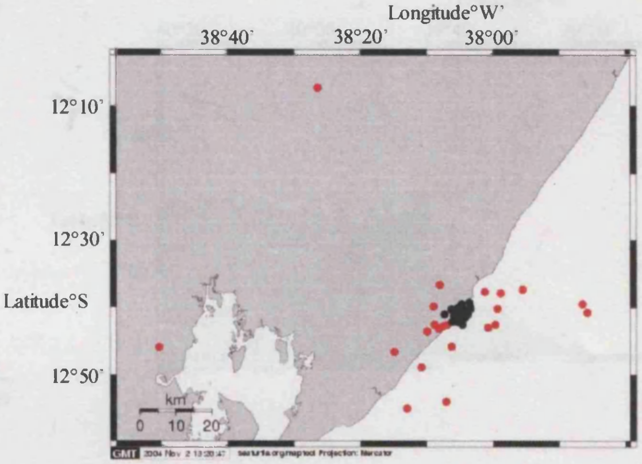


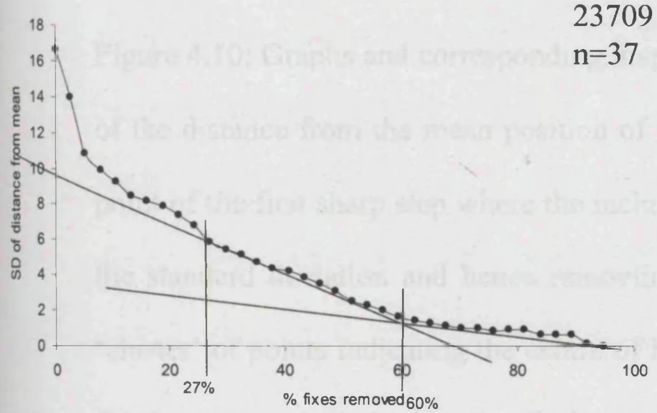
4394A
n=12



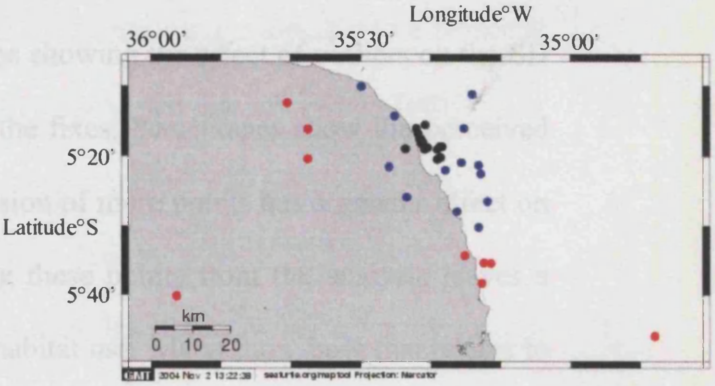


4394B
n=65





23709
n=37



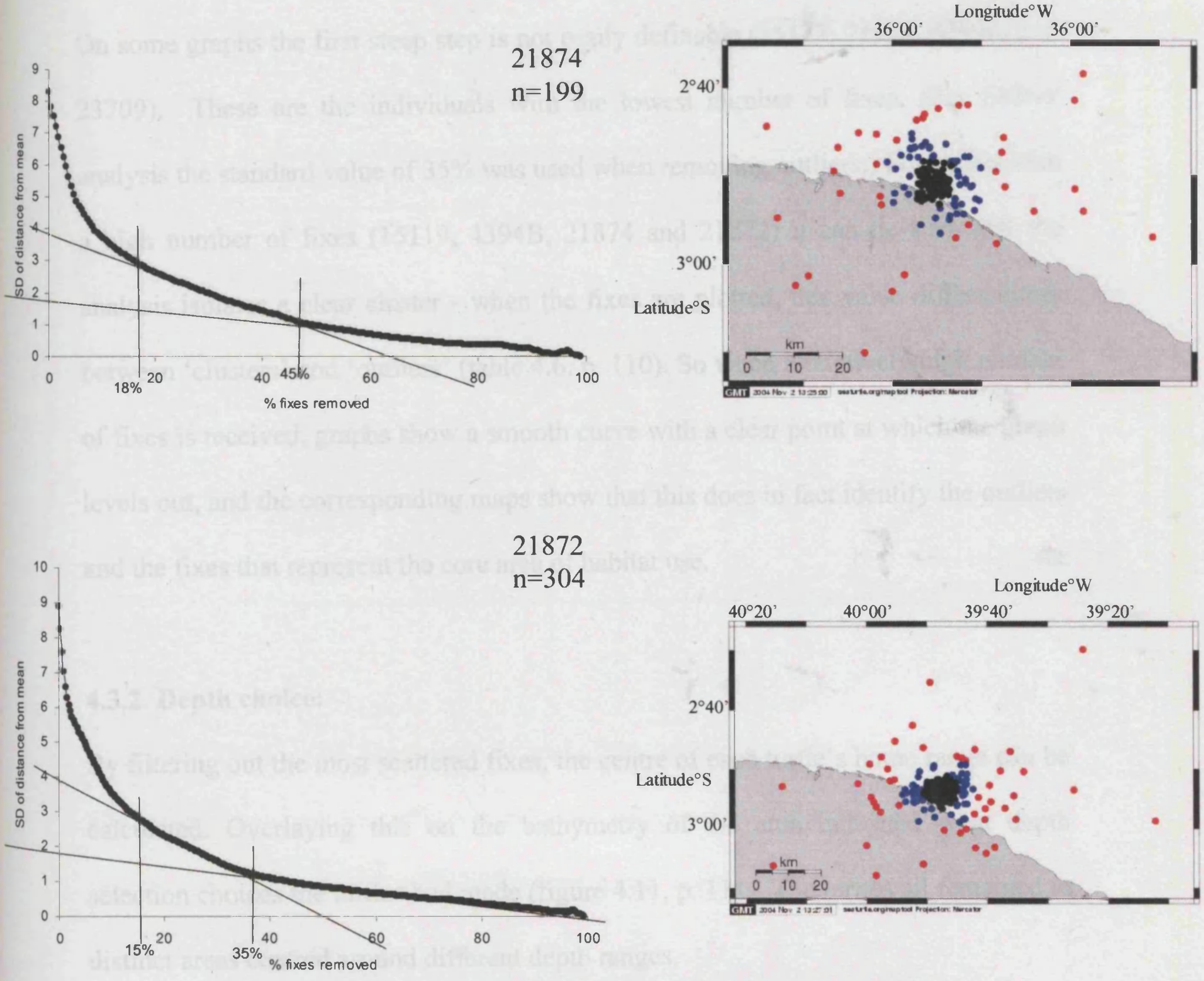


Figure 4.10: Graphs and corresponding maps showing the effect of outliers on the SD of the distance from the mean position of the fixes. Percentages show the perceived point of the first sharp step where the inclusion of more points has a greater effect on the standard deviation and hence removing these points from the analysis leaves a 'cluster' of points indicating the centre of habitat use. Maps show how this relates to the data set, red circles are the furthest outliers, blue circles if present indicate the secondary outliers whilst black circles are the main cluster.

On some graphs the first steep step is not easily definable (15122, 21914, 4394A and 23709). These are the individuals with the lowest number of fixes. (For further analysis the standard value of 35% was used when removing outliers.) For turtles with a high number of fixes (15119, 4394B, 21874 and 21872) it can be seen that the analysis isolates a clear cluster - when the fixes are plotted, this value differentiates between 'clusters' and 'outliers' (table 4.6, p. 110). So when a relatively high number of fixes is received, graphs show a smooth curve with a clear point at which the graph levels out, and the corresponding maps show that this does in fact identify the outliers and the fixes that represent the core area of habitat use.

4.3.2. Depth choice:

By filtering out the most scattered fixes, the centre of each turtle's home range can be calculated. Overlaying this on the bathymetry of the area indicated what depth selection choices the turtles had made (figure 4.11, p. 111). The turtles all remained in distinct areas centred around different depth ranges.

The methods used here to filter the fixes and provide a centre of home range can be confirmed for turtles with a diving record, by comparing the depth taken from the bathymetry maps with the maximum depth of dives performed by the turtles. The SMRU transmitters attached on Ascension Island in 2001 provided 6 h summaries of diving behaviour from which average depth can be calculated. Comparing this average depth with the bathymetry shows a definite relationship, confirming the location filtering and the centres of the home range (figure 4.12, p. 112).

Individual	**No of fixes**	**Fixes in cluster (%)**
15119	79	70
15122	*58*	*
21914	*49*	*
4394A	*12*	*
4394B	65	65
23709	*37*	*
21874	199	55
21872	304	65

Table 4.6: Number of fixes used for identifying cluster and the percentage retained after analysis to remove outliers. * indicates turtles where the standard value of 65% was used due to a lower number of fixes with less well defined results.

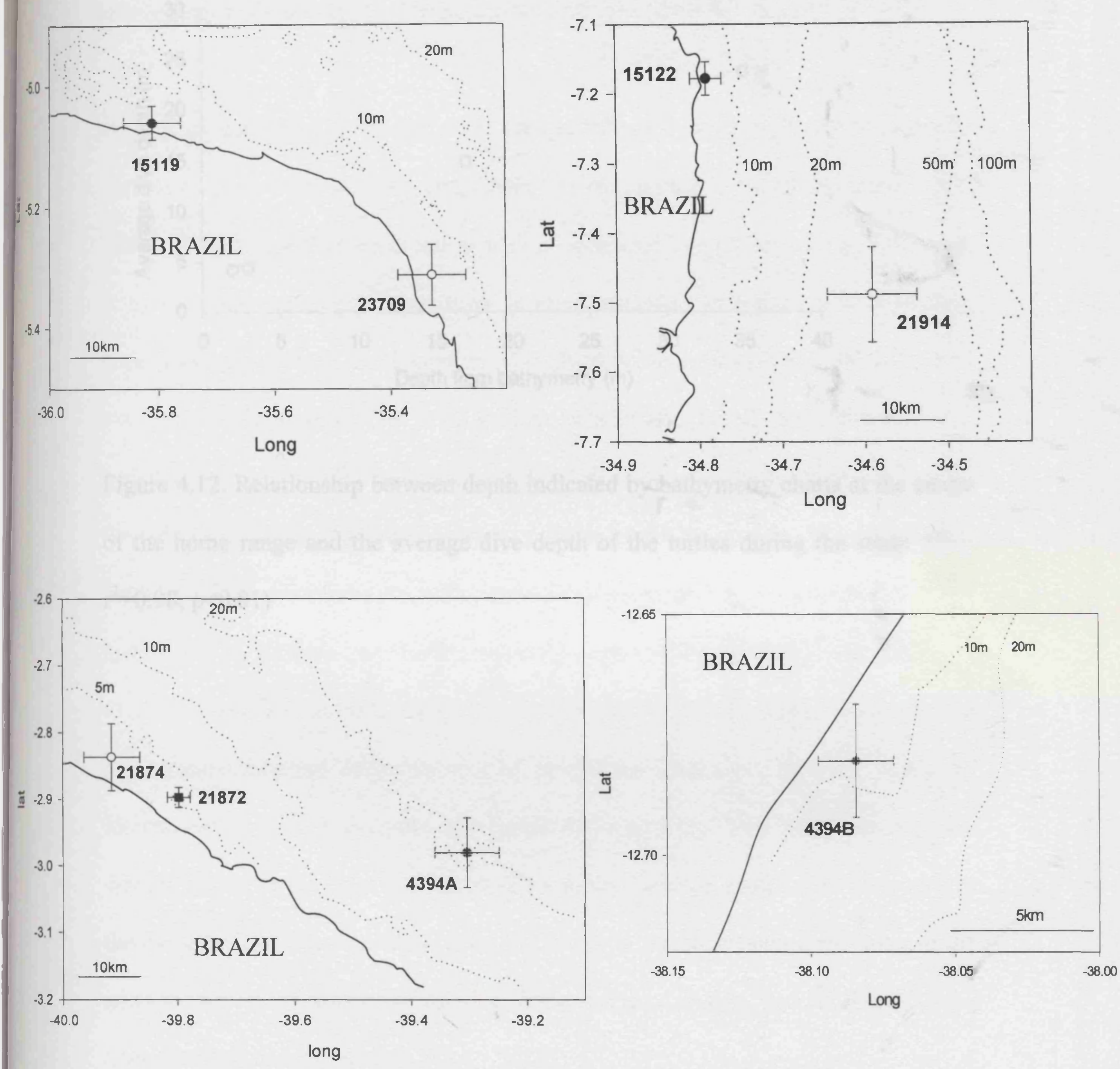


Figure 4.11i-iv: The range centres (mean position ± 1SD) for the turtles that were resident off the coastline of Brazil. Solid line indicates the coast and dotted lines represent the depth contours.

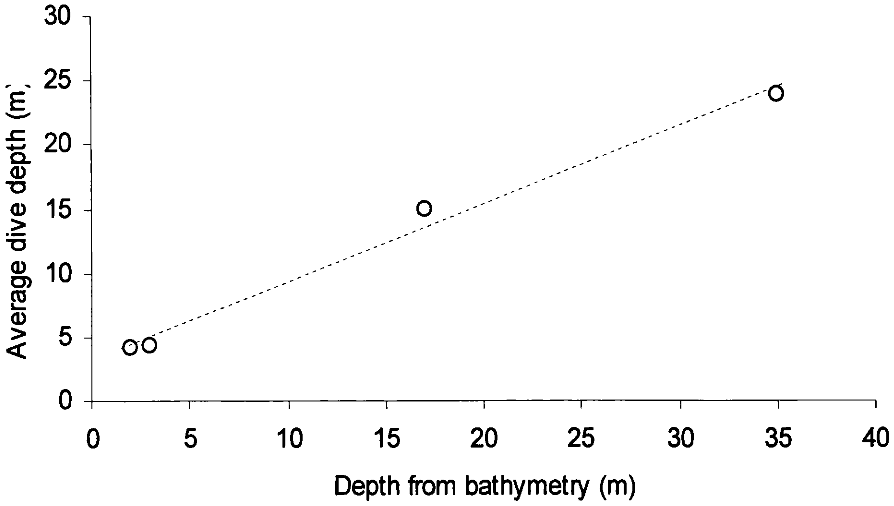


Figure 4.12. Relationship between depth indicated by bathymetry charts at the centre of the home range and the average dive depth of the turtles during the study. ($F_{1,2}$, r^2=0.98, p<0.01)

4.3.3. Home range size:

As some of the fixes in these clusters are still seen to be overland, there must be some satellite error still involved in the calculated locations (table 4.7, p. 114).

To give an indication of the size of the habitat utilised by each turtle, the biologically unrealistic fixes were removed first, (those that would imply a travelling speed over 5 kmh^{-1}). There is still considerable scatter of locations (see earlier section - 4.3.1, p. 101). Previous studies have quantified the error associated with fixes of each location class using transmitters in a known fixed position on land. Hays et al. (2001b) carried out a trial with transmitters at a similar latitude and found that latitudinal and longitudinal values differ in a bivariate distribution around the mean. The standard deviation seen in the observed locations of the turtles off the coast of Brazil represents the sum of the error inherent with Argos calculations and actual movement by the turtles. So to separate out the importance of each factor, a macro was written in Minitab to create plots with a range of theoretical values for animal movement against the summed standard deviation seen by animal movement and inputted values for transmitter error (for example see figure 4.13, p. 115). The value for standard deviation seen in the observed scatter of locations was read across from the *y*-axis to the curve and the corresponding value on the *x*-axis was the standard deviation of the animal movement for each satellite error value. Latitude and longitude were considered separately for each LC.

As these transmitters were not tested in a fixed known position, the mean of the fixes with outliers removed was used as the central position. The standard deviation was examined for all the fixes and then the outliers were removed and the calculation was

Individual	**LC**	**No. of inland fixes**	**Distance from nearest coastline (km)**		
			Mean	**S.D.**	**Range**
15119	B	24	19.15	27.74	0.57-92.23
	A	3	6.84	8.63	1.6-16.79
15122	B	19	6.99	6.85	0.6-27.8
	A	2	2.28	2.28	0.67-3.89
21914	B	8	10.61	4.42	1.19-14.42
	A	2	33.62	4.67	30.32-36.92

Table 4.7: The distance of inland fixes from the nearest coastline. For 3 individuals, the LC and number of fixes inland, the mean distance of these fixes from the nearest coastline (km), the SD and the range. An indication of the level of accuracy of the location classes can be indicated from the distance of any fixes calculated as being inshore from the nearest coastline. As the turtle cannot be inland, the minimum error for each location is the straight line distance from the nearest coastline to the position of the fix.

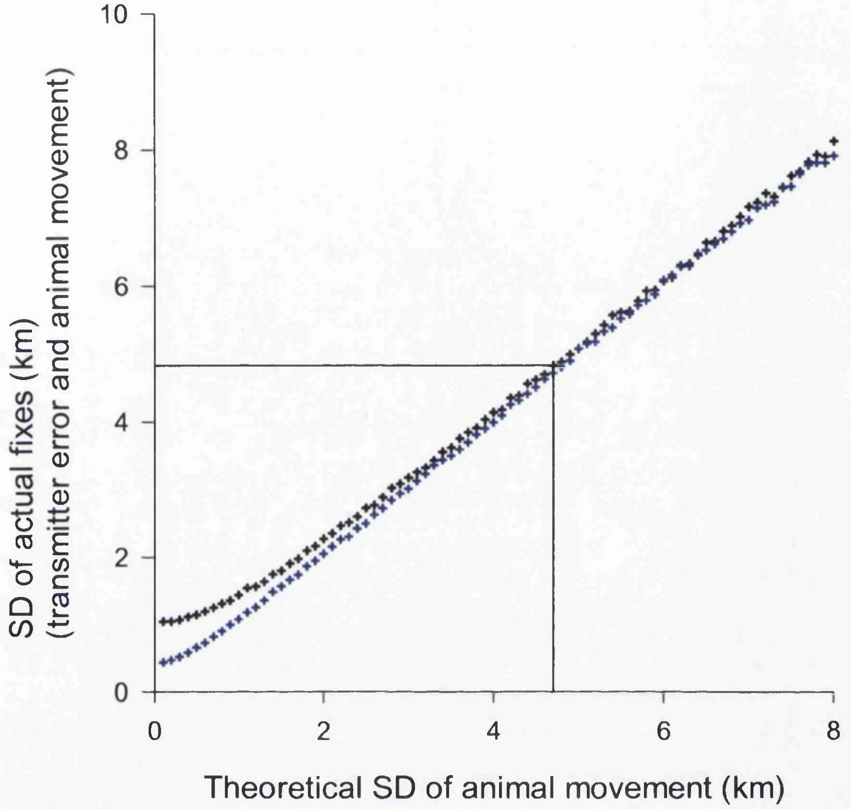


Figure 4.13: Example of graph used to identify the biological movement using the error calculated for satellite-derived locations by Hays et al. (2001b) (black symbols) and Vincent et al. (2002) (blue symbols). This graph shows the latitudinal distribution of LC1 using values reported in Hays et al. (2001b) and Vincent et al. (2002) of 1.03 km and 0.43 km respectively. The example shown is for individual 21914, where the latitudinal SD for LC1 fixes was 4.77 km (n=3). Reading across the graph this equates to animal movement with SD of 4.7 km (for both transmitter error values). Further analyses used values from Hays et al. (2001b) as these were calculated at a similar latitude to this study.

repeated. Using the cluster of points identified earlier is a way of quantifying the core area of habitat use without influence from any outliers. In some cases, even before filtering for outliers, the value seen for the SD of the Argos fixes in this study was less than that reported for satellite-derived error alone in Hays et al. (2001b) (table 4.8, pp. 117-118). This was particularly the case when examining the core area, implying restricted movement by most of the turtles.

The CCL was measured for most of the turtles during the attachment procedure (table 4.9, p. 119). No weight measurements were taken during the Ascension attachment, so this was calculated from the equation in Hays et al. (2002):

$$\text{Mass (kg)} = 3.75\ \text{CCL} - 258$$

These body mass values need to be regarded as approximate values. The regression was calculated for the relationship between length and mass of fasting turtles at Ascension Island. It is possible that depending on the length of time these turtles stayed at Ascension Island after attachment, the energy demands of the variable length post-nesting migration and any subsequent opportunistic foraging behaviour, that the mass to length ratio would change between individuals.

There was no significant relationship seen here between the size of the turtle and the depth choice seen at the foraging area (figure 4.14, p. 120) nor a relationship between the size of the turtle and the area of habitat use calculated here ($p>0.05$). However, there was a significant positive relationship between the size of the habitat use and the depth shown by the bathymetry at the centre of this (figure 4.15, p. 120).

Turtle	LC		Standard Deviation (km) (ALL FIXES)				Standard Deviation (km) (OUTLIERS REMOVED)			
			N	Observed	Fixed trial	Calculated	N	Observed	Fixed trial	Calculated
15119	1	lat	3	5.1	1.03	5	2	1.09	1.03	0.3
		long		10.31	1.62	10.3		0.63	1.62	X
	A	lat	11	2.36	1.39	1.9	10	2.49	1.39	2
		long		7.86	0.81	7.8		5.55	0.81	5.5
	B	lat	65	7.65	5.23	5.5	44	3.26	5.23	X
		long		13.82	7.79	11.3		5.44	7.79	X
15122	A	lat	15	4.81	1.39	4.7	12	1.82	1.39	1.2
		long		2.23	0.81	2.1		1.31	0.81	1
	B	lat	42	10.6	5.23	9.2	25	3.07	5.23	X
		long		8.65	7.79	3.6		2.27	7.79	X
21914	1	lat	3	4.78	1.03	4.7	3	4.78	1.03	4.7
		long		1.19	1.62	X		1.19	1.62	X
	0	lat	10	13.35	4.29	12.6	6	7.13	4.29	5.7
		long		13.39	15.02	X		3.44	15.02	X
	A	lat	10	22.44	1.39	22.5	5	10.65	1.39	10.6
		long		26.56	0.81	26.6		3.02	0.81	2.9
	B	lat	26	14.05	5.23	13.1	18	7.32	5.23	5.1
		long		12.48	7.79	9.9		7.13	7.79	X
4394A	0	lat	2	4.44	4.29	1.3	2	4.44	4.29	1.1
		long		4.64	15.02	X		4.64	15.02	X
	A	lat	3	42.56	1.39	42.9	2	5.32	1.39	5.2
		long		78.47	0.81	78		2.28	0.81	2.2
	B	lat	7	8.7	5.23	6.9	4	4.59	5.23	X
		long		15.34	7.79	13.3		8	7.79	1.5
4394B	A	lat	16	1.37	1.39	X	16	0.76	1.39	X
		long		1.51	0.81	1.3		0.73	0.81	X
	B	lat	46	11.43	5.23	10.2	24	1.56	5.23	X
		long		16.4	7.79	14.6		1.46	7.79	X

			Standard Deviation (ALL FIXES)				Standard Deviation (OUTLIERS REMOVED)			
Turtle	**LC**		**N**	**Observed**	**Fixed trial**	**Calculated**	**N**	**Observed**	**Fixed trial**	**Calculated**
23709	A	lat	6	3.83	1.39	3.6	6	3.83	1.39	3.6
		long		3.19	0.81	3.1		3.19	0.81	3.1
	B	lat	30	16.59	5.23	15.6	17	6.25	5.23	3.5
		long		22.22	7.79	20.9		7.54	7.79	X
21874	1	lat	2	0.47	1.03	X	2	0.47	1.03	X
		long		2.2	1.62	1.5		2.2	1.62	1.5
	A	lat	23	2.75	1.39	2.4	18	1.74	1.39	1.1
		long		2.74	0.81	2.6		1.2	0.81	0.9
	B	lat	173	6.96	5.23	4.5	89	1.97	5.23	X
		long		9.39	7.79	5.3		1.77	7.79	X
21872	2	lat	2	0.16	0.28	X	2	0.16	0.28	X
		long		0.39	0.62	X		0.39	0.62	X
	1	lat	6	1.04	1.03	0.1	6	1.04	1.03	0.1
		long		1.64	1.62	0.3		1.64	1.62	0.3
	A	lat	20	4.01	1.39	3.8	15	1.59	1.39	0.8
		long		6.2	0.81	6.2		1.32	0.81	1.1
	B	lat	275	6.11	5.23	3.2	17	1.71	5.23	X
		long		9.79	7.79	6		2.23	7.79	X

Table 4.8: For each individual, the number of fixes in each LC, then, calculated separately for latitude and longitude, the observed standard deviation from the ARGOS fixes, the standard deviation of the error predicted by Hays et al. (2001b), and then the calculated biological movement of the animal once the error has been removed from the ARGOS fixes (see text for exact method). This calculation is shown twice (once for all the fixes received and then again when the outliers have been removed), to show the difference this filtering process makes on the calculated area of movement seen for the turtles. (An 'X' indicates when the observed SD is less than the SD from the fixed trial, and hence, the calculation is not applicable.)

Turtle	**CCL (cm)**	**Mass (kg)**
15119	118	*(184)*
15122	113	*(166)*
21914	101	*(121)*
4394A	117	*(180.75)*
4394B	117	*(180.75)*
23709	92	74.5
21874	53	14.5
21872	41	6.5

Table 4.9: CCL and mass for turtles foraging off the coast of Brazil. Mass values in parentheses are values calculated from the CCL using the equation in Hays et al. (2002) not actual measurements. (No values available for Mediterranean turtles.)

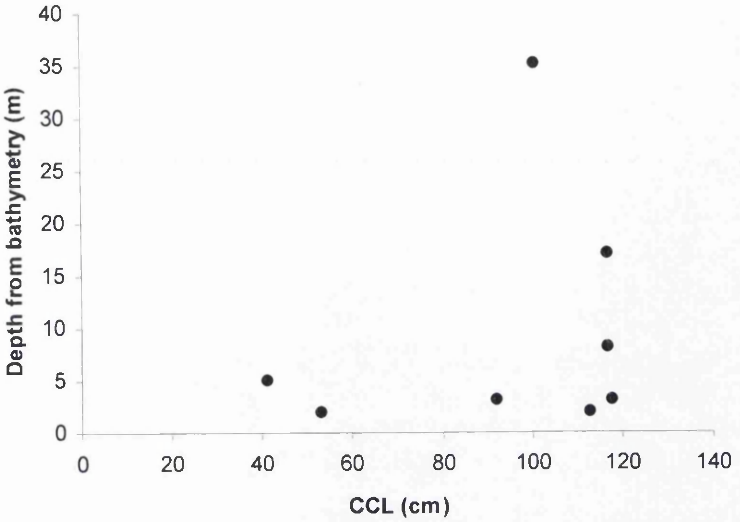


Figure 4.14: Curved carapace length of the turtle and the depth at the centre of its home range.

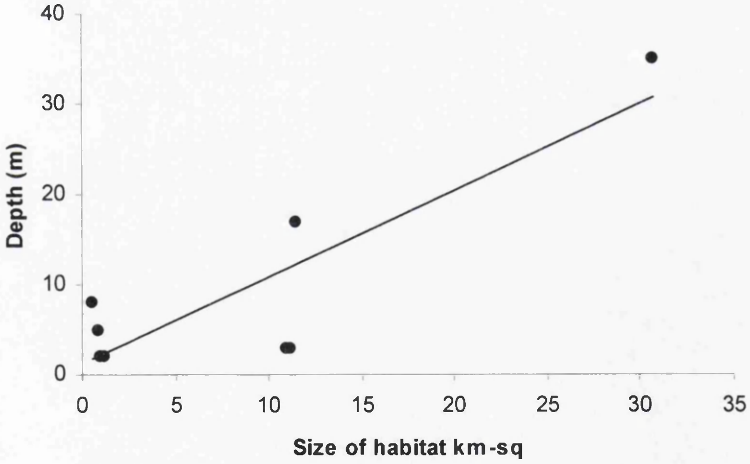


Figure 4.15: Relationship between the depth shown by bathymetry at the centre of the home range and the size of this core area of habitat use. (values shown are the movement seen using LCA fixes) (For n = 8; Bathymetry depth = 1.27 + 0.954 size; $r^2 = 0.73$, $F_{(1,6)} = 16.59$, $p<0.01$)

CHAPTER 5

Diving Behaviour: Dive Profiles, Changes During Migration and at Foraging Grounds

5. Diving behaviour: dive profiles, changes during migration and at foraging grounds.

5.1. Defining the dive types:

Dive shapes were classified following work in Houghton et al. (2002), Hochscheid et al. (1999), Minamikawa et al. (1997) and Seminoff et al. (2006), where different numbers of dive shapes were distinguished depending on the detail of the study (figure 5.1, p. 123).

TDR studies of green turtles at Ascension Island have shown that the highest proportion of time is spent engaged on U-shaped dives during internesting (figure 5.2C, p. 123) or midwater dives when travelling (figure 5.2A, p. 123) (Hays et al., 2000a & 2001a). These dives have distinct shapes and to decide what variables to use when allocating a dive type to the profiles in this study, it was decided what criteria are used when visually classifying dive type. The midwater dives have a steep initial descent phase to the maximum dive depth followed by a slow ascent phase and then a final steep ascent (figure 5.1, p. 123; types 3&4). In order to select these dives it would be predicted there would be a negative depth change between the first and last inflection points and that the r-squared value for the bottom phase would be high due to the slope of the gradual ascent phase. In a number of studies, the time spent within 2 m of the maximum depth of the dive has been used as a parameter to separate U-dives from other dive shapes. In Martin (2003) U-dives were delineated by having a value greater than 85%, whilst Hays et al. (2000a) found that dives could be considered U-shaped dives if greater than 90% of the dive duration was spent within 2

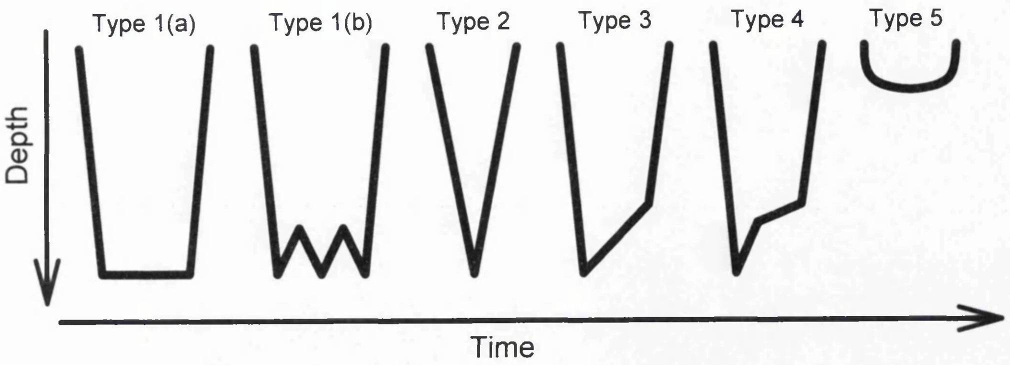


Figure 5.1: Generalised profiles for the 6 dive types undertaken by green turtles (from Seminoff et al. (2006). Type 1(a) and type 1(b) are as reported for loggerhead turtles in Houghton et al. (2002).

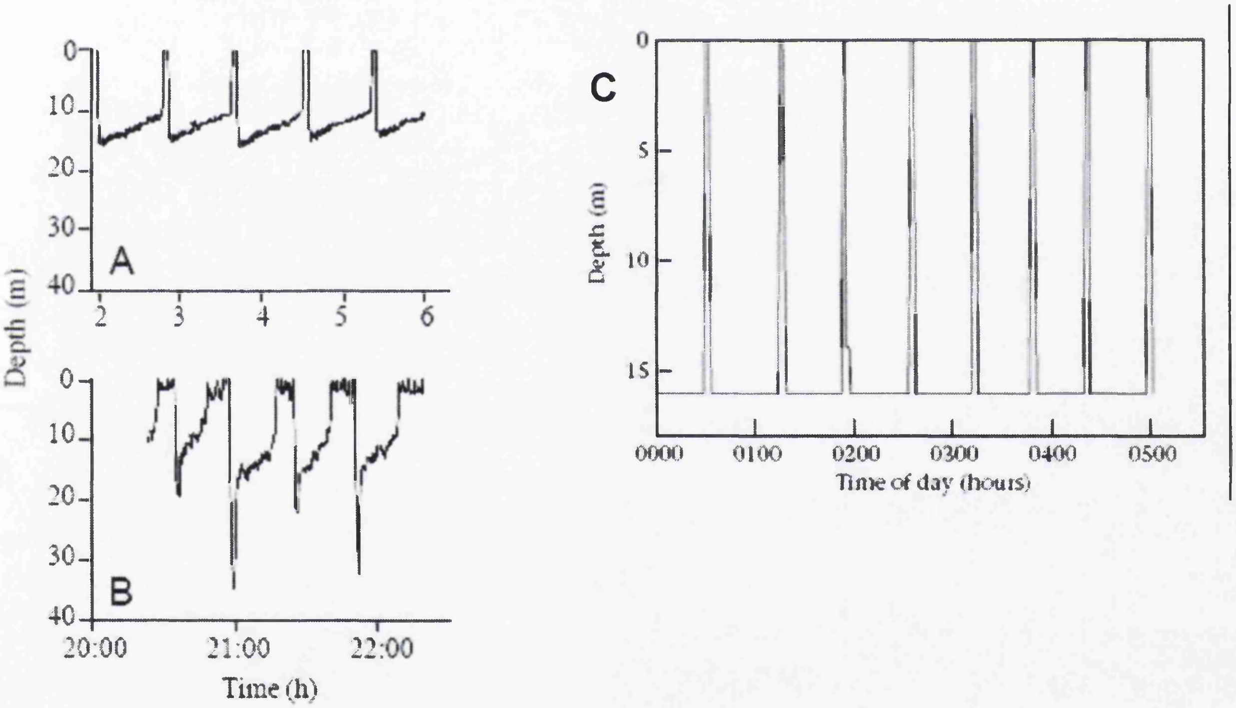


Figure 5.2: On the left, examples of (A) type 3 and (B) type 4 dives seen during migration back to Ascension Island (from Hays et al., 2001a). In both dive types, most of the dive was spent in a period of gradual ascent, with this phase being preceded by a short period of more rapid ascent for type 4 dives. On the right (C) is a typical bout of resting dives from an internesting green turtle at Ascension Island (from Hays et al., 2000a).

m of the maximum depth. Both these studies were carried out on internesting turtles around Ascension Island where the turtles were engaged in clear bouts of resting U-dives of a similar depth and duration (figure 5.2C, p. 123). Houghton et al. (2002) found that turtles engaged in active behaviour during internesting carried out some less uniform U-shaped dives with the bottom phase only representing an average of 75% of the dive duration. Hays et al. (2000a) also stated a criterion of a dive constituting a U-dive was 'there had to be no systematic linear change in depth during the flat phase of the dive profile.' This would be reflected in a low standard deviation between the depth values of the profile, a small depth change during the bottom phase (between D1 and D5) and a high value for time within 2 m of the maximum depth. Type 2 dives are not commonly seen in green turtle diving studies but would probably be detected by a very low value for the time spent within 2m of the maximum dive depth, whilst type 5 dives which are shallow travelling dives are not recorded as profiles in this study; only the depth and duration are recorded.

Due to problems with the saltwater switch, it became apparent that some surface intervals were missed and on some occasions, two dives were encoded into one profile. Also, the end points of some dives were missed and any points during a dive that were less than 6 m in depth were encoded as zero. As diving behaviour is so conservative at Ascension with a high proportion of U-shaped resting dives observed of a similar depth and duration, it is easy to divide up any profiles that are actually 2 dives or identify a missed end point. At foraging areas where behaviour is more varied, this cannot be done with such certainty (see example in figure 5.3, p. 125).

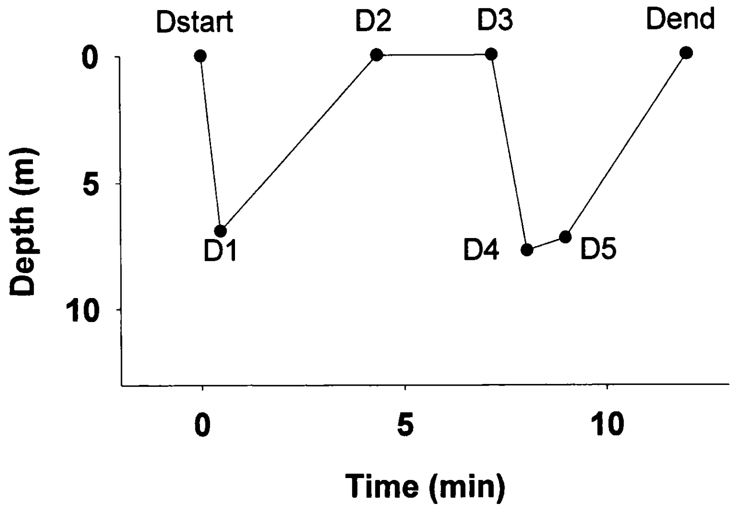


Figure 5.3: An example of a shallow dive profile recorded for 15119 during the period of the study at the foraging ground. The 5 dive inflection points (D1 to D5) are shown with zero values recorded for D2 and D3.

A total of 2006 profiles was recorded for the 7 turtles, and after removing any with zero depth readings less than 10 m deep, the data set included 1101 profiles (table 5.1, p. 127). In order to try and allocate a dive type to each profile, any dives that included zero depth values were initially excluded from the analysis. The following ten parameters were tabulated in Minitab for each remaining profile: maximum dive depth, dive duration, percentage of the total dive time spent within 2 m of the maximum depth, r-squared of the linear regression for the time and depth of the inflection points, standard deviation of the 5 depth values, change in depth seen during the bottom phase (D1 to D5), duration of descent phase as a percentage of total dive duration, duration of bottom time as a percentage of total dive duration, duration of ascent phase as a percentage of total dive duration and the ratio between depth and duration. A macro was written so that each profile could be visually inspected to confirm dive type allocation. Principal component analysis (correlation matrix) was conducted using these ten dive variables to see if distinct groups could be identified. This analysis indicated two main groupings (figure 5.4, p. 128). To elucidate if the two groupings correspond to different shaped dive profiles, dives were selected at random from the data set and visually examined to see if they fitted the typical U-shaped or type 3 profiles seen in TDR studies. The residual value for each was checked as a low value implies that the dive profile provided was a good fit for the actual shape of the dive. Ten dives were selected for both U-shaped and type 3 dives. By overlaying the component scores for the 20 selected dives, it can be seen that the two clusters may correspond to these two dives types (figure 5.5, p. 128) suggesting the majority of diving seen here corresponds to that seen in other studies where U-dives and midwater type 3 dives dominate. The analysis showed that dive parameters strongly associated with the first two principle components were standard deviation of

Individual	**Number of dive profiles**				
	Total	**Complete**	**Contains at least one zero depth**	**Invalid (all depths=0)**	**Invalid (erroneous values)**
4394A	72	**18** *(25%)*	49 *(68%)*	3 *(4%)*	2 *(3%)*
4395	135	**81** *(60%)*	51 *(38%)*	3 *(2%)*	0 *(0%)*
15119	527	**306** *(58%)*	197 *(37%)*	24 *(5%)*	0 *(0%)*
15120	128	**85** *(67%)*	40 *(31%)*	3 *(2%)*	0 *(0%)*
15121	123	**51** *(42%)*	68 *(55%)*	4 *(3%)*	0 *(0%)*
15122	594	**326** *(55%)*	243 *(41%)*	25 *(4%)*	0 *(0%)*
21914	427	**234** *(54.8%)*	154 *(36%)*	38 *(9%)*	1 *(0.2%)*
TOTAL	2006	**1101** *(55%)*	802 *(40%)*	100 *(5%)*	3 *(0%)*

Table 5.1: The quantity and quality of the dive profiles received. For each individual and for all turtles combined, the total number of profiles received, and then, the number that had 5 depth values greater than zero, that contained at least one zero depth reading, where all depth readings were zero and those that had unrealistic data values. Values in parentheses are the percentage of the total number of dives for that individual.

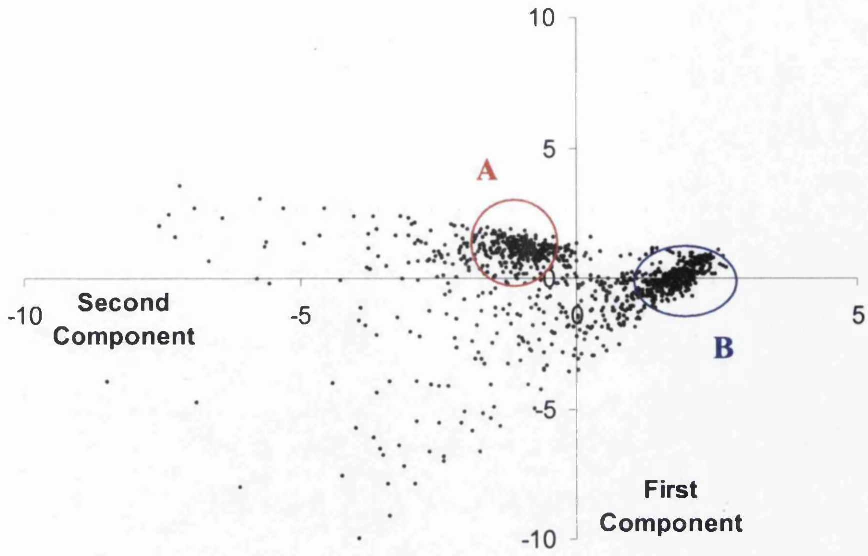


Figure 5.4: Plot of the first two principal components after analysis on ten dive parameters using all dive profiles that do not include a zero depth reading for all turtles (n=1101 dives). Circles highlight two apparent clusters A and B.

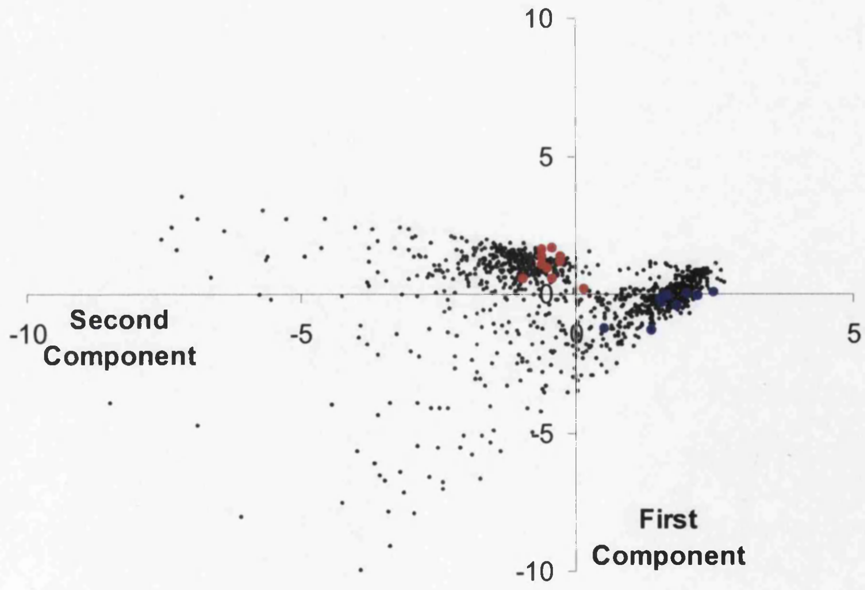


Figure 5.5: As figure 5.4 but with values highlighted in each cluster A and B for ten randomly selected type 3 and ten U-shaped dives. ● Type 3 dives, ● U-shaped dives

the depth values, time within 2 m of the maximum dive depth and depth change during the dive. As predicted, these two types of dives showed clear differences for these parameters (figure 5.6, p. 130).

The entire data set of dive profiles that did not contain a zero depth value (n=1101) was then sorted to select all the U-dives and type 3 dives using the parameters identified above. First, all dives with a SD value of zero were clearly U-dives (n=103). The profiles that included over 90% of the dive time spent within 2 m of the maximum depth were also identified as U-dives (n=333). From the values associated with the type 3 dives examined so far, dives were selected that had less than 50% time within 2 m of the maximum depth, had a depth change between 5 and 20 m during the dive and also had a high r-squared value (>0.70) implying a steady ascent phase. These dives all showed the typical midwater dive profile (n = 288). Of the remaining 340 profiles, those that had a standard deviation less than 0.5 were U-dives (n = 37), and those including over 80% within 2m of the maximum depth were also U-dives (n = 60). The remaining 243 were visually examined by the author to determine if they could be allocated a dive type; 24 were described as U, 38 as type 3 midwater dives, 27 as type 4 midwater dives (those with a deeper excursion during ascent) and 134 as 'others'. It may be due to the fact that 67% of these latter 243 dives had a residual value of 8 or higher (compared to 26% for the dives identified before) that the U dives and type 3 dives were not identified by the dive parameters as before. Overall, the highest proportion of dives were classified as U-dives (51%), though this varied throughout migration from 5% during the open sea phase to 83% during internesting (table 5.2, p. 131). The descriptive statistics for each dive type are presented in table 5.3 (p. 132).

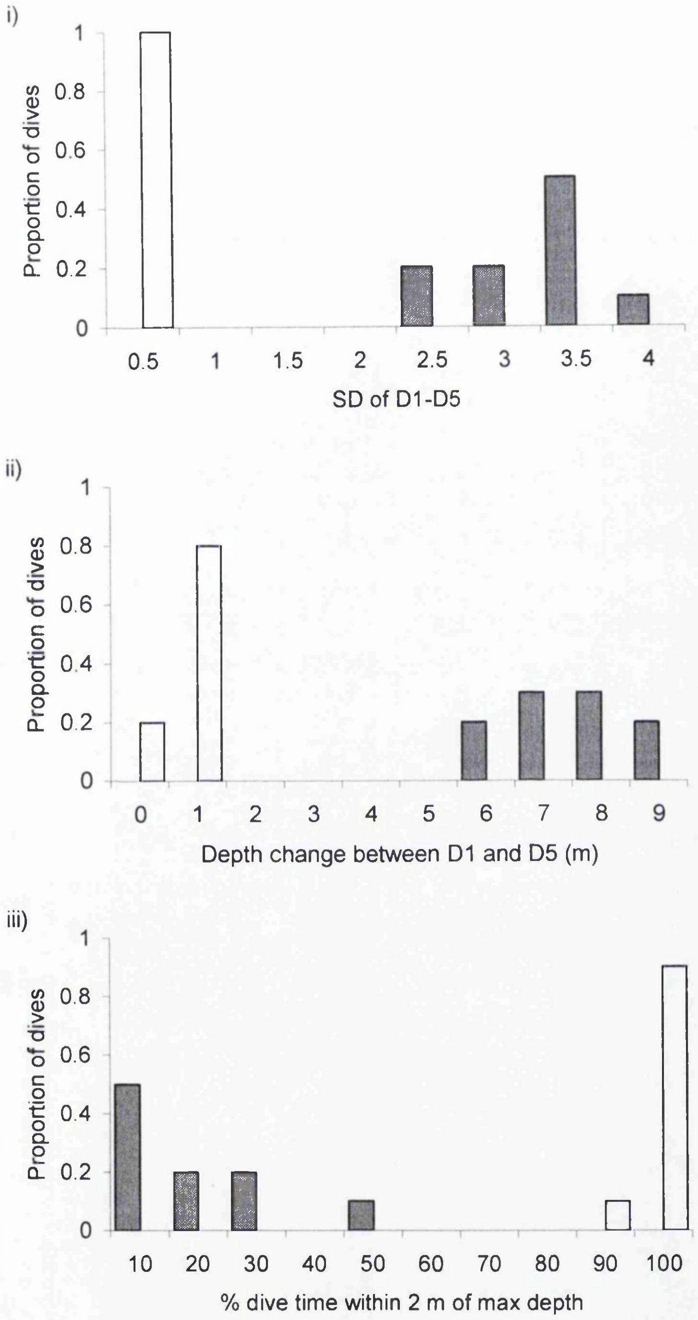


Figure 5.6: Graphical representation of the range of values for the dive characteristics that showed a clear difference between the two dive types, midwater dives (type 3) (filled bars) and U-dives (type 1) (open bars). Values on x-axis represent the upper limit of each histogram bin.

	Phase of migration				
Dive type	**Ascension**	**Open Sea**	**Coast**	**Foraging**	**Overall**
Type 1 (U)	388 (83%)	21 (5%)	66 (55%)	82 (86%)	557 (50%)
Type 3 (midwater)	7 (2%)	310 (74%)	7 (6%)	2 (2%)	326 (30%)
Type 4 (S)	- -	20 (5%)	7 (6%)	-	27 (2%)
Other	71 (15%)	70 (16%)	40 (33%)	11 (12%)	192 (18%)
Total	**466**	**421**	**120**	**95**	**1102**

Table 5.2: Quantity of the dive types identified for each phase of migration and overall. Values in parentheses are the percentage of the total number of dives for each phase. (This analysis excluded any dive profiles that had a zero depth reading.)

	Dive type			
Dive characteristic	**Type 1 (U)** **n=557**	**Type 3 (midwater)** **n=326**	**Type 4 (S)** **n=27**	**Other** **n=191**
Maximum depth (m)	16.5 ± 5.51	17.4 ± 2.94	33.3 ± 11.7	17.2 ± 6.11
Duration (min)	36.3 ± 14.3	28.8 ± 6.35	27.2 ± 6.53	18.1 ± 10.5
Time within 2m of max depth (%) *	72.4 ± 4.13	21.1 ± 11.2	8.54 ± 5.14	32.5 ± 16.6
r2 of inflection points	0.27 ± 0.27	0.89 ± 0.10	0.57 ± 0.16	0.34 ± 0.26
SD of D1-D5 (m)	0.06 ± 2.95	7.37 ± 1.88	16.4 ± 11.2	2.72 ± 5.89
Depth change between D1 and D5 (m)	0.61 ± 1.31	3.20 ± 0.94	9.29 ± 4.95	3.26 ± 2.25
Descent as % dive time *	10.0 ± 1.79	9.75 ± 1.54	12.6 ± 4.78	12.0 ± 4.53
Bottom time as % dive time *	72.4 ± 2.82	72.9 ± 3.14	64.9 ± 13.0	65.0 ± 10.2
Ascent as % dive time *	14.2 ± 2.50	13.8 ± 2.99	20.2 ± 13.8	21.0 ± 9.86
Maximum depth/duration	0.55 ± 0.39	0.65 ± 0.26	1.28 ± 0.52	1.34 ± 1.02

Table 5.3. Mean values (±1 SD) for the 4 types of dive identified from the dive profile record for dive characteristics chosen that were predicted to delineate between the dive types. *All percentage values have been arcsine transformed to satisfy normalisation criteria.

In order to provide more profiles for analysis especially in the foraging areas, some dives with a zero value for the final inflection point were corrected. Turtle 15119 was very close to the shore once resident at the foraging ground and hence it would be inaccurate to adjust the dives in this way. Of 82 dive profiles recorded at the foraging area, only 7 (8%) did not contain at least one zero value, reflecting the shallow habitat of the turtle, implying that these readings could be inflection points between the surface and 6 m and not necessarily missed end points (mean maximum depth for profiles at the foraging ground is 7.99 m.) The same was seen for turtle 15122, where the number of dives containing zero readings was also high (n=100; 81%). This turtle was also very close to the shore and the mean depth of all the recorded profiles was 9.30 m. An additional 74 profiles can be added to the data set, 14 for 4394A, 7 for 15119, 4 for 15121, 6 for 15122 and 43 for 21914. These were classified as 41 U-shaped dives, 1 S-dive, 5 midwater type 3 dives and 27 'other' dives. The total number of profiles available for analysis is presented in table 5.4 (p. 134).

The U-dives were examined to see it they could be divided further as in Houghton et al. (2002). The largest data set of U-dives at the foraging area is for turtle 21914 (n=64). When PCA is carried out on these dives, it indicates 2 groups. When these are examined, the two groups agree with those seen in Houghton et al. (2002) termed (U)a and (U)b. U(a) dives show a sharp descent followed by a long flat bottom phase and then a short final descent. Type U(b) have a similar profile but the ascent and descent phases are not as steep and hence less time is spent on the bottom phase. The latter dives also show more variation in the bottom phase. (For descriptive statistics see table 5.5, p. 135.) The depth/duration ratios are significantly different for the two groups, implying that for the same depth U(a) dives have longer durations implying

		Dive type				
ID	**Phase**	**Type 1**	**Type 3**	**Type 4**	**Other**	**Total**
15119	Ascension	156	1	0	32	**189**
	Sea	0	70	1	5	**76**
	Coast	22	2	0	17	**41**
	Foraging	6	0	0	1	**7**
	Total	**184**	**73**	**1**	**55**	**313**
15120	Ascension	65	2	0	8	**75**
	Sea	5	0	0	3	**8**
	Coast	0	0	0	0	**0**
	Foraging	2	0	0	0	**2**
	Total	**72**	**2**	**0**	**11**	**85**
15121	Ascension	3	1	0	1	**5**
	Sea	1	33	1	3	**38**
	Coast	1	6	3	2	**12**
	Foraging	5	40	4	6	**55**
	Total	**10**	**80**	**8**	**12**	**110**
15122	Ascension	82	1	0	13	**96**
	Sea	5	158	8	35	**206**
	Coast	2	0	0	1	**3**
	Foraging	22	0	0	5	**27**
	Total	**111**	**159**	**8**	**54**	**332**
21914	Ascension	16	0	0	4	**20**
	Sea	10	48	10	23	**91**
	Coast	50	3	3	29	**85**
	Foraging	64	2	0	15	**81**
	Total	**140**	**53**	**13**	**71**	**277**
4394	Sea	0	1	0	1	**2**
	Coast	8	0	1	5	**14**
	Foraging	12	1	1	2	**16**
	Total	**20**	**8**	**2**	**2**	**32**
4395	Ascension	66	2	0	13	**81**

Table 5.4: Description of dive profiles received. For each individual, the number of type 1 (U), type 3 (midwater), type 4 (S) and 'other' dives received for each phase of migration and overall.

Group	N	Descent phase	Bottom phase	Ascent phase	Standard deviation
		(percentage of dive duration) *			
U(a)	45	10.2±1.71	71.6±2.94	15.0±2.56	0.67±1.11
U(b)	20	12.4±2.66	67.0±4.11	18.8±3.72	2.56±3.40

Table 5.5: The percentage of the total dive duration for the descent, bottom and ascent phase of the dive for each grouping of U-dives (mean ± 1SD) and the standard deviation of the depth values indicating the variation in the depth of the bottom phase.

*All percentage values have been arcsine transformed to satisfy normalisation criteria.

less activity than U(b) which are shorter at the same depths (depth/duration mean ± 1SD; U(a) 0.89±0.42, U(b) 1.77±1.14). (T_{11}=-2.67, $p<0.05$).

5.2. Dive behaviour during migration:

5.2.1. Overall patterns of dive behaviour:

Using corresponding locations, the dive data can be temporally divided into different phases of migration; the time spent at Ascension before migration, the open sea journey, coastal travel and then time at the residence areas off the Brazilian shoreline. The amount of dive data received during each phase of migration is seen in table 5.6 (p.137). There was a great variation in the amount of dive information provided by each of the SRDLs.

The depth and distribution of the individual dives recorded show changes throughout the study period. All turtles engaged in a high proportion of dives of 10 to 20m in depth whilst at Ascension and during the open sea phase, but a second peak of shallow dives is also seen in the oceanic phase. Once at the coast of Brazil dive behaviour shows much more inter-individual variation and then at the foraging area two different patterns emerge; 2 turtles engage in a high proportion of short and shallow dives whilst for the other 2, deeper and longer dives dominate.

The 6 hour summaries provided information on the time spent on dives greater than 6 m in depth and also the mean depth of deep dives and the mean depth of shallow dives. From this the average depth during the 6 hour period could be calculated as follows:

		Amount of dive information (n)					Amount of dive information (n)		
PTT	**Phase of Migration**	**Summaries**	**Profiles**	**Shallow**	**PTT**	**Phase of migration**	**Summaries**	**Profiles**	**Shallow**
15119	Ascension	36	223	28	**21914**	Ascension	5	28	5
	Sea	38	103	189		Sea	62	181	141
	Coast	12	95	12		Coast	29	87	8
	Foraging	20	82	136		Foraging	10	94	16
15120	Ascension	16	101	12	**4394A**	Ascension	-	-	-
	Sea	4	22	12		Sea	2	12	13
	Coast	-	2	-		Coast	10	29	1
	Foraging	-	-	-		Foraging	4	26	5
15121	Ascension	2	7	1	**4395**	Ascension	20	132	19
	Sea	24	91	84		Sea	0	0	-
	Coast	-	21	7		Coast	-	-	-
	Foraging	-	-	-		Foraging	-	-	-
15122	Ascension	36	143	27					
	Sea	58	300	219					
	Coast	10	4	0					
	Foraging	34	123	118					

Table 5.6: Quantity of data received during each phase of migration for the seven SRDLs attached to green turtles nesting on Ascension Island in 2001.

$$\text{Average depth in 6 hours} = (\%\text{time deep} \times \text{average deep depth}) + (\%\text{time shallow} \times \text{average shallow depth})$$

Although the 6-hour summaries do not give great detail about diving behaviour as they only provide mean values, they are very useful to confirm the conclusions drawn from examination of the dive profiles and give an overall indication of the changes in behavioural patterns. This is particularly useful in this tracking study due to the paucity of data provided from some individuals. The diving behaviour changes markedly between the different migration stages and between the individuals. A high proportion of time is engaged on deep diving (dives over 6 m depth) during the time spent at Ascension Island (mean percentage of time = 79.2 %, n = 6 individuals) and very few shallow dives are recorded, whilst more time is spent nearer the surface during the oceanic phase of migration reflected in a higher number of shallow dives (mean number of shallow dives in 6hours ± SD for 6 individuals; Ascension 1.4±1.1, sea 30.6±14.0). The coastal phases show more variety between the individual turtles. Then 2 distinct patterns emerge in the foraging areas reflecting the depth choices seen with a similar overall behavioural pattern between turtles 15119 and 15122 which engage in a high number of shallow dives and have a lower mean depth compared to 4394A and 21914.

The time during the 6 hour periods spent engaged in dives over 6 m in depth is a useful indication of whether the lack of dive profiles received from some individuals is simply due to a lack of uplinks or transmitter failure, or that the turtle is engaged in diving behaviour that would not be recorded as profiles (i.e. dives only in the top 6 m of the water column.) Although the number of dive summaries received from the foraging grounds is low, the average percentage of time diving over 6 m in depth reflects the average dive depth of the turtles in shallow water (see table 5.11, p173). The average depth values from the summaries can also confirm the depth selection implied from the bathymetry charts (regression of average diving depth versus depth from bathymetry: $F_{1,2}=178.47$, $r^2=0.99$, $p<0.01$).

5.2.2: Diving behaviour at Ascension Island:

The diving behaviour of these turtles during the internesting period has been described in detail in Martin (2003). The 4 turtles that renested after attachment showed typical internesting behaviour dominated by U-dives (83% of all dive profiles recorded) with a median depth of 14.2, 16.2, 17.6 and 17.6m for turtles 4395, 15119, 15120 and 15122, respectively. These are inferred as resting dives due a lack of foraging opportunities around Ascension Island. Swim speed data provided for the turtles during internesting validates this as the speed during the bottom phase is virtually zero compared to the descent phase. This is opposed to the non U dives which show an active bottom phase with a swimming speed of around 50% of the descent phase.

5.2.3: Open sea diving behaviour:

There are two main groups of dive profiles seen during the open sea migration, midwater dives with a typical 'type 3' phase and variable 'other' shaped dives. A small number of S-shaped type 4 dives and U dives are also seen. It is immediately apparent when looking at the dive profile record that the open sea phase is dominated by dives of a classic type 3 shape (74% of dive profiles overall, range 53-92% for 4 individuals). Figure 5.7 (p. 140) shows an example of a bout of dives with this shape.

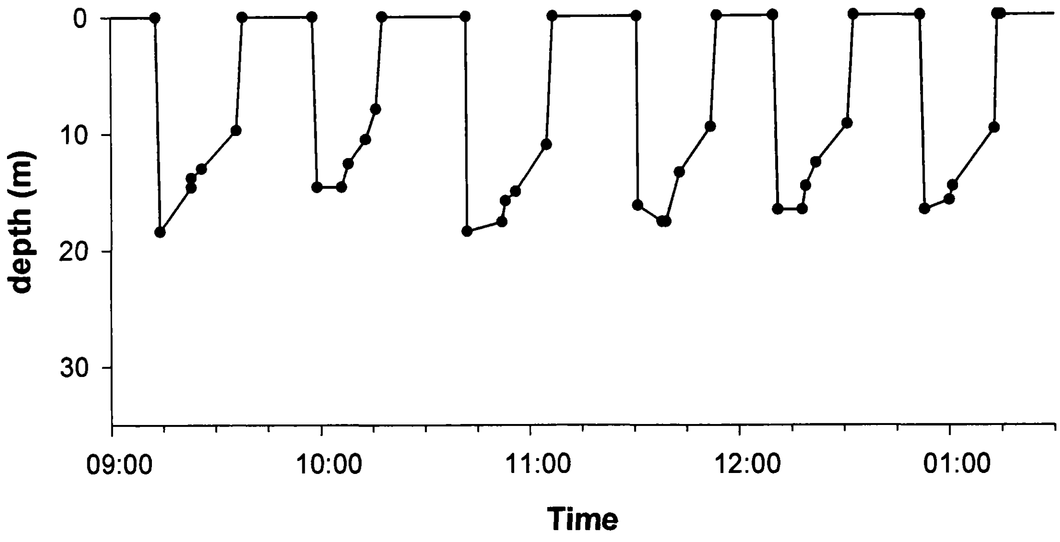


Figure 5.7: Example of a bout of type 3 midwater dives taken from the dive profile record of individual 15119 during the open sea phase of post-nesting migration.

During the ocean crossing the depth of these dives remains relatively constant for each turtle whereas they all show a gradual increase in duration except 21914 (figure 5.8, p. 142). This may be due to the fact that 21914 stopped during migration near Fernando de Noronha (3°51'S, 32°25'W) and conducted U dives. This may affect the overall diving pattern of this individual compared to the other turtles. There is no significant relationship between the mean depth or duration of the midwater dives and the size of the turtles.

As seen in other studies, there is a diel pattern in the frequency of those distinctive midwater dives (figure 5.9, p. 143). Dive profiles were predominantly recorded at night implying shallow diving behaviour less than 6 m in depth during daytime hours. This is confirmed by the 6 hour summaries (figure 5.10, p. 144). For all individuals there are a high proportion of the midwater dives during the night as they crossed the ocean compared to other dives which are seen during daytime. The type 3 dives are significantly longer in duration than 'other' midwater dives (figure 5.11, p. 145) (mean±SD; type3 dives: 28.94±5.96 min, other dives: 19.15±9.66 min) (t-test: $T_{75}=7.92$, $p<0.001$) and the depth/duration ratio is significantly larger, implying type 3 dives are less active than the 'other' dives (t-test: $T_{65}=-4.73$, $p<0.001$).

Swim speed data were obtained for 3 turtles during this phase, with adequate data (i.e. non-zero values) provided for 92 type 3 and 24 'other' dives. Unfortunately, all the sensors had ceased providing data before the turtles had reached the coast of Brazil. The descent phase was used as a benchmark value to compare with the other 2 dive phases, as the turtle must be actively swimming down the water column to overcome

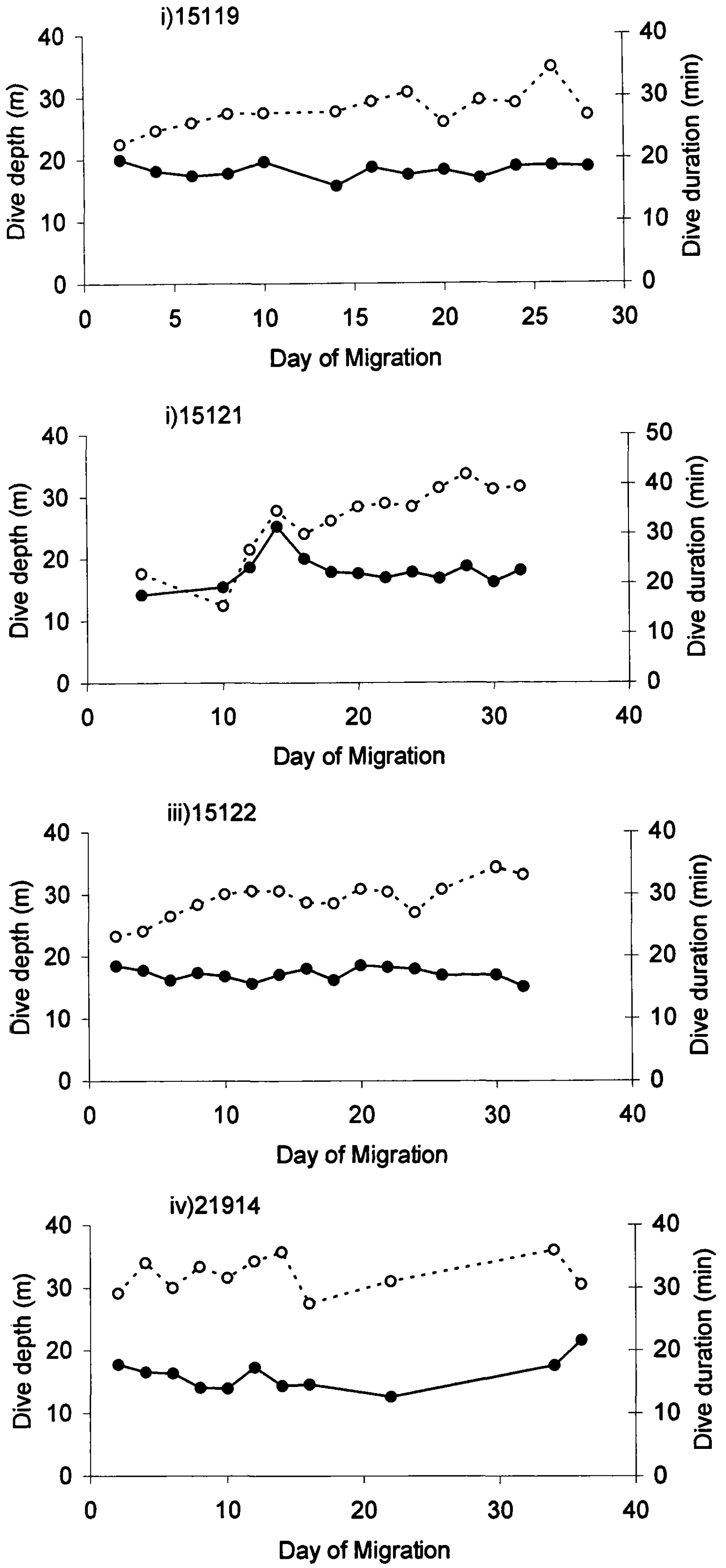


Figure 5.8: The mean depth (●) and duration (○) of midwater type 3 dives for two day intervals during the open sea phase of migration for turtles i) 15119, ii) 15121, iii) 15122 and iv) 21914.

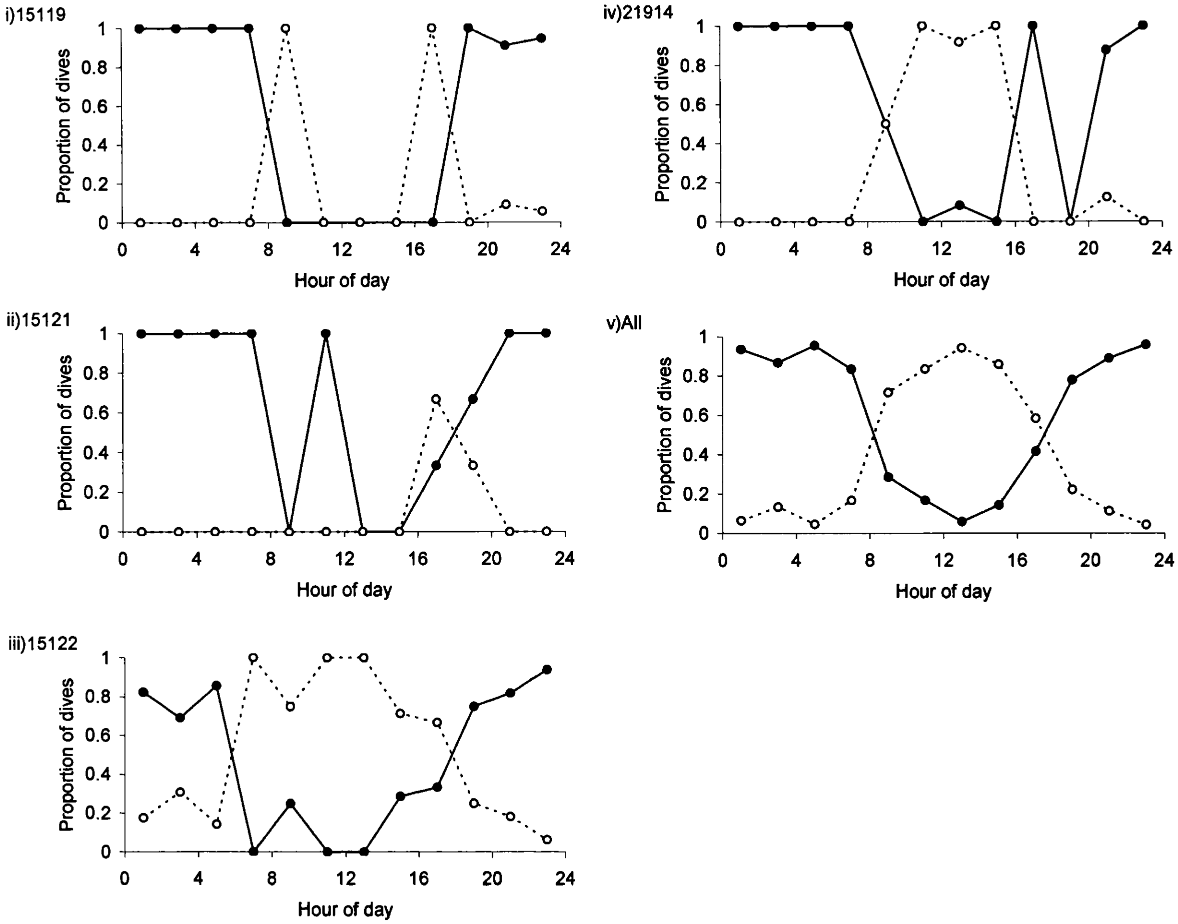


Figure 5.9: Relative proportion of midwater type3 dives (●) and other dives (○) in two hour intervals throughout the open sea crossing for i) 15119, ii) 15121, iii) 15122, iv) 21914 and v) all turtles combined.

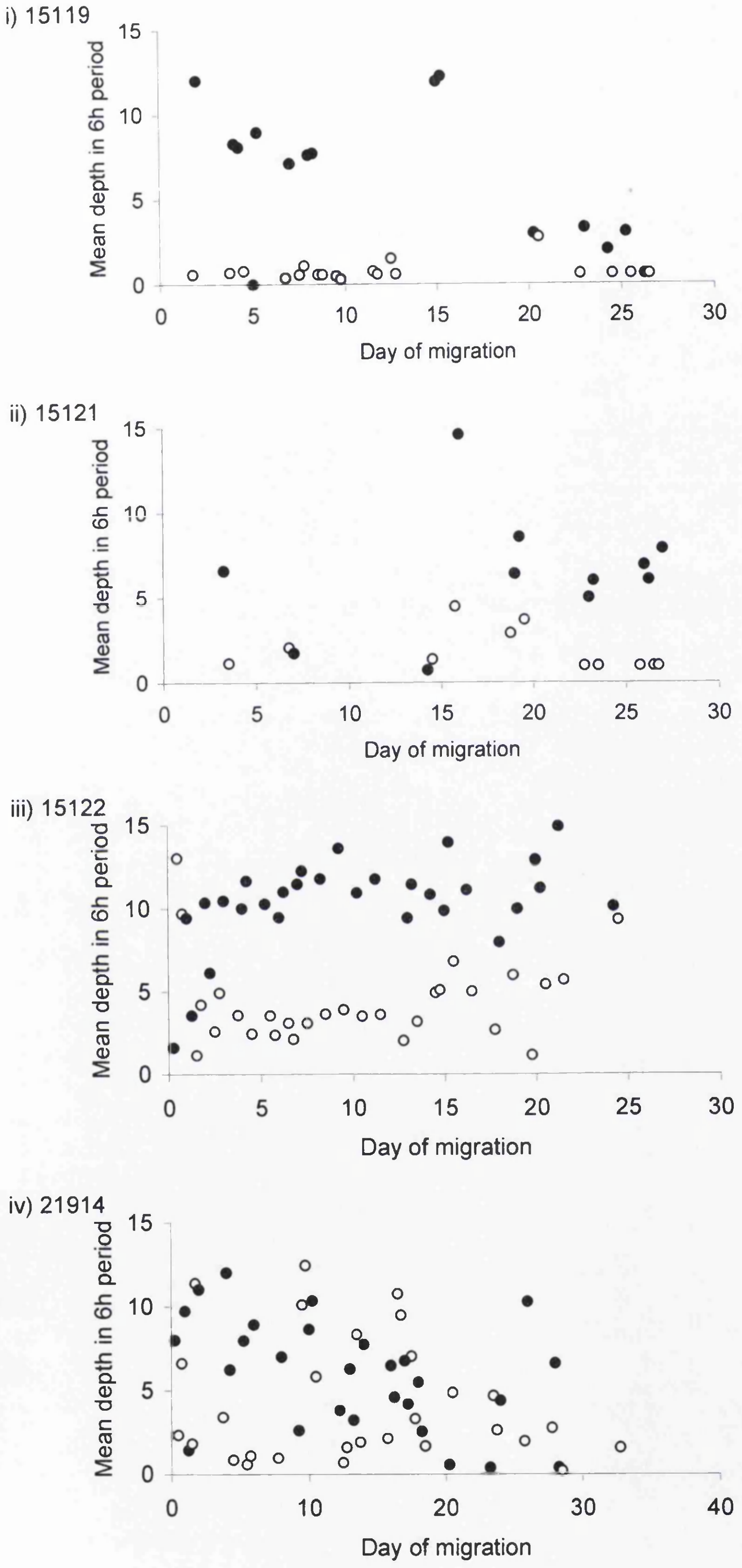


Figure 5.10: Mean dive depth during the open sea phase of migration for 6 hour periods that are predominantly during night time (●) (8pm to 8am local time) and daylight hours (○) (8am to 8pm local time).

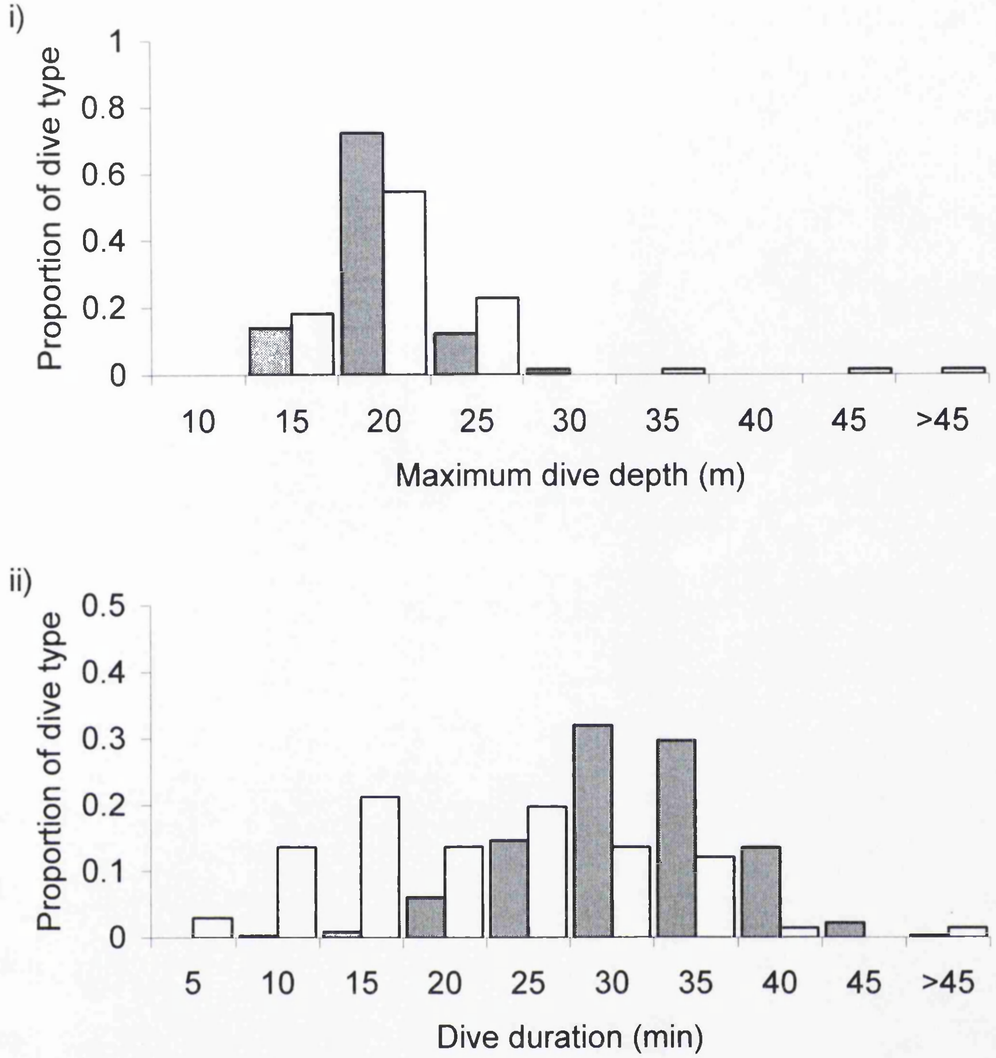


Figure 5.11: The distribution of i) dive depth and ii) dive duration for 'other' dives (open bars) and type 3 dives (filled bars) during the open sea crossing phase of migration for 4 individuals.

the positive buoyancy associated with a lung full of air. When comparing the bottom phase with the value for descent, it can clearly be sent that type 3 dives showed an active bottom phase compared to the U dives at Ascension (figure 5.12, p. 147). When the mean speed was calculated for each dive, U dives at Ascension were clearly inactive dives with very low values, whilst during type 3 dives, the turtles engaged in active movement. The 'other' dives showed a much more variable range of speeds than type 3 dives (figure 5.13, p. 147.) The mean speed of type 3 dives showed a significant relationship with the depth of these dives but not with duration (regression: mean speed=0.0173 maximum dive depth + 0.120; $F_{1,90}=16.2$, $r^2=0.15$, $p<0.001$.)

5.2.4: Approach to shallow waters:

As these turtles approach the coast of Brazil, a dramatic change in behaviour occurs. In many cases very deep dives, greater than 50 m in depth, are seen and the types of dives conducted change markedly. Unfortunately, no speed sensor data are available by this time of migration, but overall speed of travel decreases as the turtles reach the shallower waters indicating a change in behaviour.

Data were examined for 10 days either side of the point where the location data indicates arrival close to the coast of Brazil in order to isolate any changes in behaviour associated with the approach to shallow waters. For most of the turtles behaviour was initially dominated by midwater dives with the typical profile of a steep descent, followed by a gradual ascent and then a final steep ascent phase. A series of deep dives were seen for 3 of the turtles, followed by shallower dives and predominance of U-shaped dives (figure 5.14, p. 148).

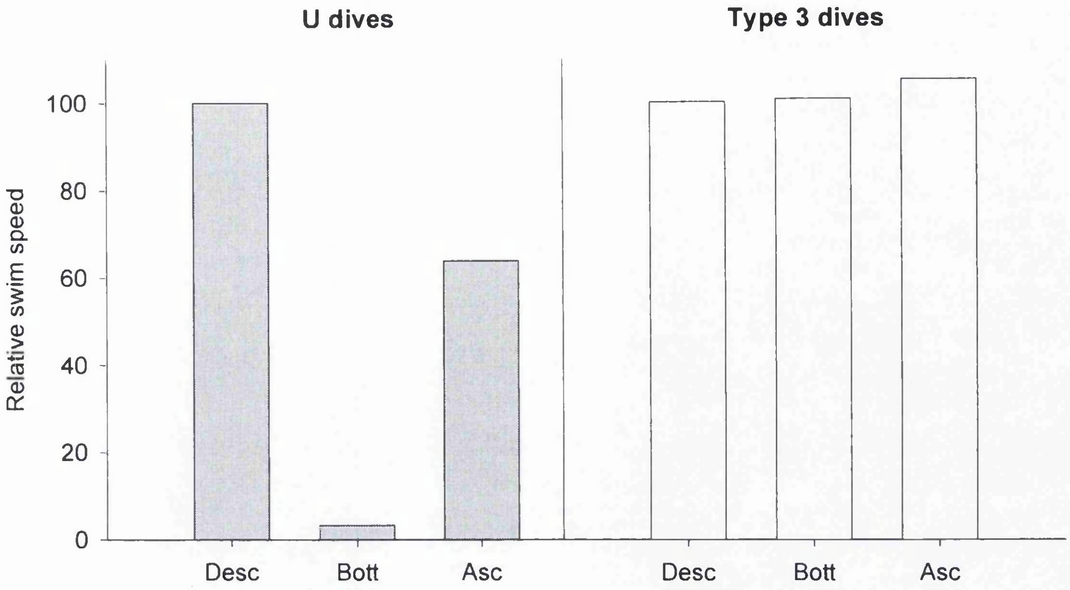


Figure 5.12: Relative swim speed of descent, bottom and ascent phases of U dives at Ascension Island (filled bars) and type 3 dives (open bars) during the open sea phase; (the descent speed always equals 100).

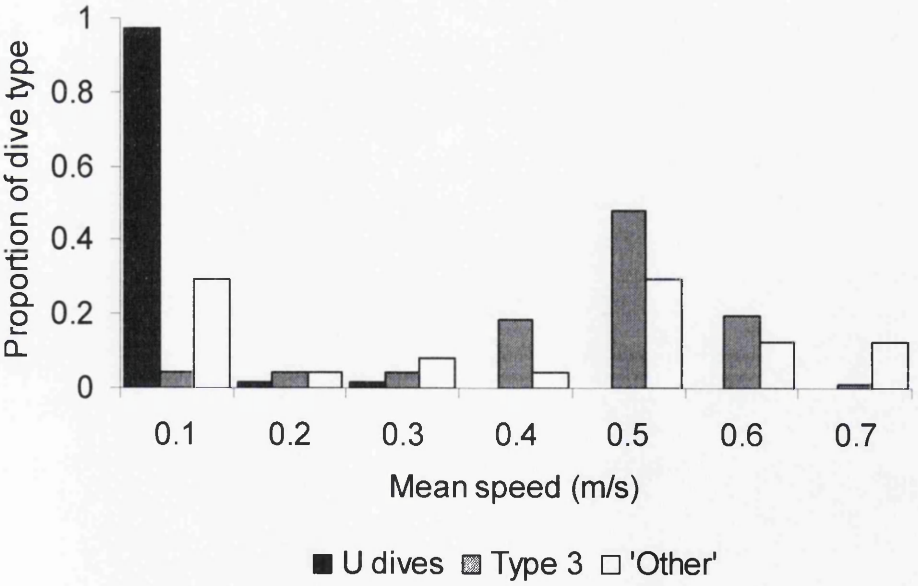


Figure 5.13: Distribution of the mean speed of dives. Graph shows the proportion of dives of each type for U dives at Ascension Island, and type 3 and 'other' dives during the open sea phase.

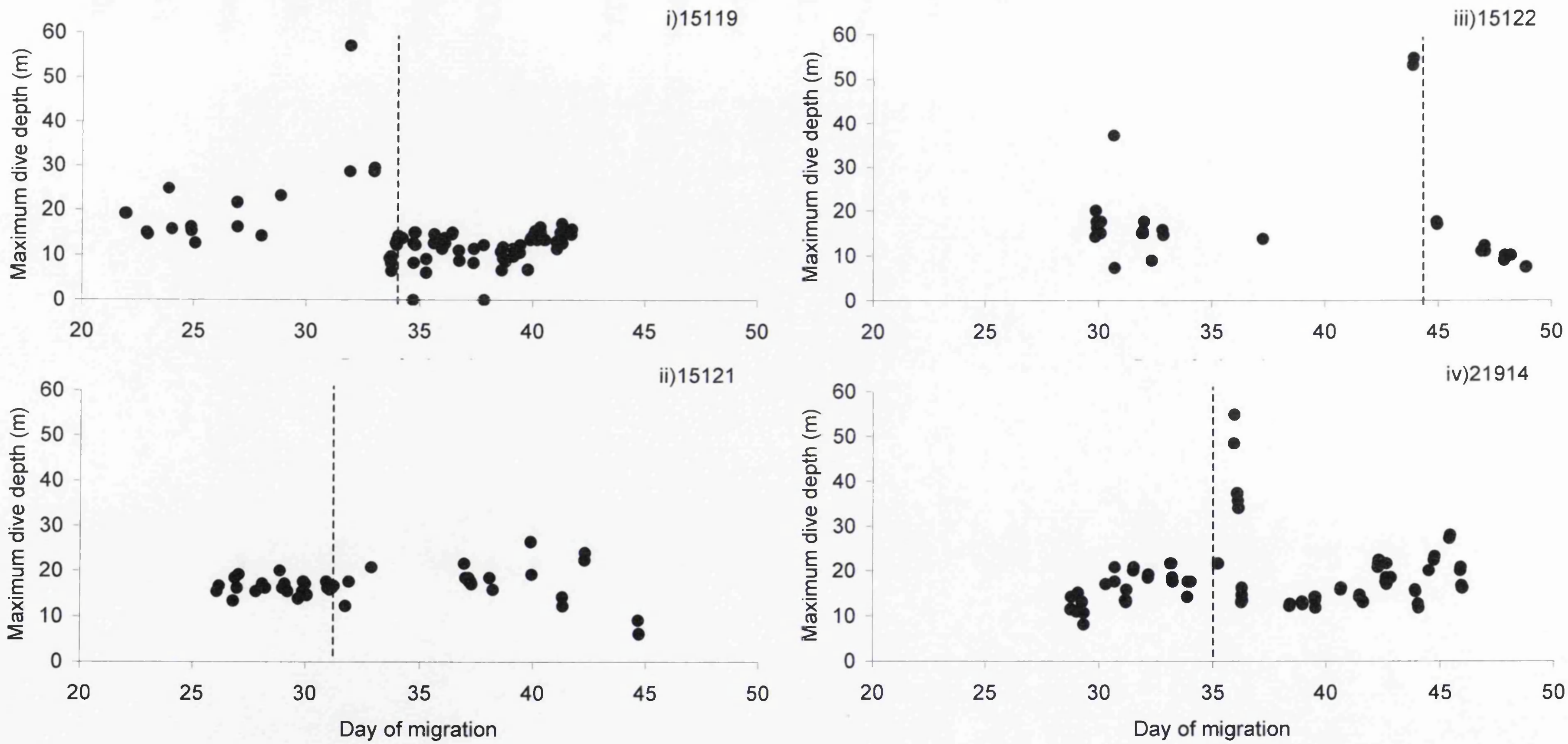


Figure 5.14: The maximum dive depth of profiles recorded for 10 days either side of the arrival close to Brazil, showing the presence of deep dives for turtles i)15119, iii)15122 and iv)21914. (Dashed line indicates approximate date of arrival in coastal waters.)

For turtle 15119, the location data implied the coast was reached around 14/7/01 (day 34 of migration), so for analysis data were selected from 10 days before and after this date; i.e. from 4/07/01 to 24/7/01 inclusive. Dive profiles recorded were exclusively midwater (type 3) dives with a relatively narrow depth and duration range, until a series of deep dives were seen, over 28 m deep. At this point it can be assumed that the coastline is reached as dives become consistently shallow, mean 12.13 m, range 6.1-17 m. The depth distribution against time clearly indicates the point at which the shallow water is reached and diving changes.

For 15121, the location data implied the coast was reached around the 03/7/01 (day 31 of migration), so data were selected for examination between 24/6/01 and 12/7/01. Again diving was initially dominated by midwater dives with a narrow depth range 13.4-20.8 m. Data were not provided for the 3 days at the time the coast would have been reached, and no deep diving was observed. There is not such a clear delineation between sea and coastal travel, though the depth of dives does become more varied as the turtle enters waters off Brazil.

There is only a short coastal migration for turtle 15122, as she reached the coast of Brazil close to the area in which she became resident for the remainder of this study. The location data imply the coast is reached around the 24/7/01 (day 44 of migration), though a paucity of data around this time makes this a little uncertain, so data were selected from 11/7/01 to the 31/7/01 to insure that the transition point was included. Up until 19/7/01 the diving was dominated by midwater dives, generally 13.8-20 m deep. Then two very deep dives are seen of 53.3 and 54.8 m.

Location data places turtle 21914 close to the coast of Brazil around the 14/8/01 (day 35 of migration). It has to be noted that this turtle conducts post-migration differently than other turtles, travelling via shallow water habitats during the open ocean migration and engaging in resting or feeding U-shaped dives before reaching the coast of Brazil. Even so, a series of deep dives, greater than 30 m are seen around the dates that the turtle appears close to Brazilian waters. Before the deep diving occurs, diving behaviour is a mixture of U-shaped and type 3 midwater dives and then after the deep dives, U-dives dominate. Apart from the deep diving, this turtle appears to conduct dives of a consistent depth range during the final open sea stage and the beginning of coastal travel.

A visual representation of some of the deep dives seen as the turtles approached the waters off the coast of Brazil reflects the variety of dive profile shapes seen (figure 5.15, p. 151). In TDR studies, these deep dives tend to be S-shaped type 4 dives, but here only 7 out of 16 (44%) could be described as this shape (the rest are classified as 2 'U-shaped' dives, 1 as '2 dives with surface missed' and 6 as 'other' shaped dives). The deep dives are recorded as occurring during night time hours (94% (15 out of 16) are conducted between 21:00 and 5:00). The deepest dive seen during the approach to Brazil is 57.2 m, and the longest was 47.5 min. It appears that these deep dives may occur in bouts. Even with the paucity of data received, 6 deep dives over 34 m in depth were recorded in succession for turtle 21914, with surfacing intervals of 1 to 1.5 min in between (figure 5.16B, p. 152). Another 2 deep dives are recorded in succession earlier that night, with a 1.5 min interval between (figure 5.18A, p. 152). Individual 15122 conducts 2 dives to over 50 m with only a 2 min surfacing between.

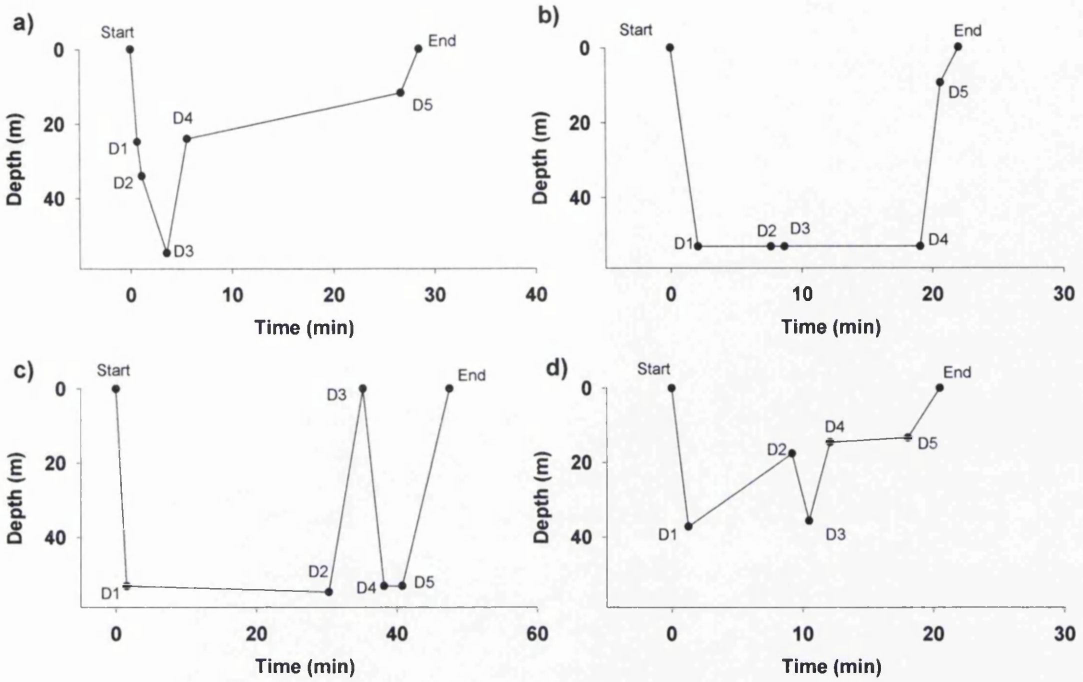


Figure 5.15: Examples of the profiles seen for deep dives including; a) typical 'S-shaped' dive; b) deep 'U-shaped' dive; c) 2 dives with surface missed, perhaps 2 U-shaped dives and d) dive classified as 'other' without a definable profile.

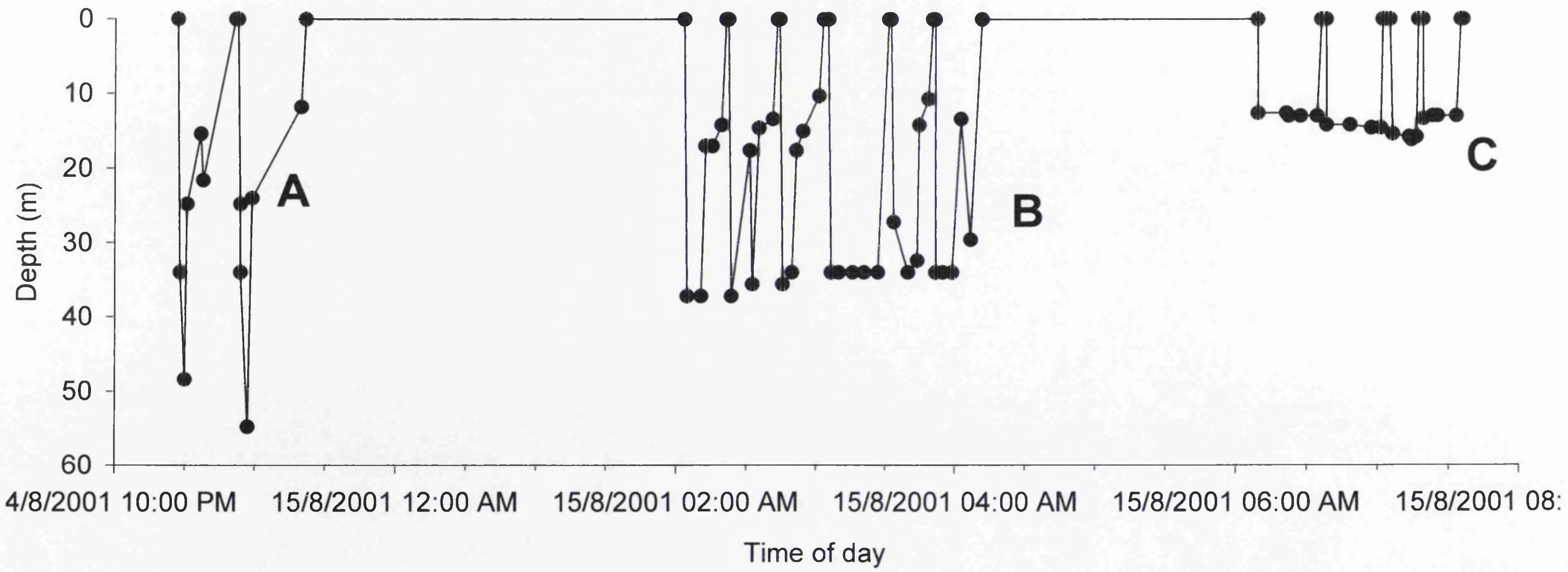


Figure 5.16: The dive profile record as 21914 approaches the coastline of Brazil on day 35-36 of migration showing A: 2 deep type 4 (S-shaped) dives followed by B: a bout of 6 dives all over 34 m in depth and then C: U-shaped dives which then dominated behaviour in coastal waters.

Although significantly deeper than other type 3 midwater dives seen during the approach to Brazil (t-test; $p<0.001$, $T_{15}=8.21$), the deep dives are significantly shorter (t-test; $p<0.005$, $T_{20}=3.24$) (descriptive statistics in table 5.7, p. 154).

5.2.5: Diving behaviour during coastal travel:

The diving behaviour is much more variable during coastal travel than during any other phase of the study. The highest proportion of dives are U dives (55%) followed by variable shaped 'other' dives (33%). The U dives and non U dives are all within a small depth range implying the turtles dive close to the seafloor during migration when conducting all dive types. The summary data are sufficient in quantity for 21914 to confirm that the recorded profiles reflect the typical diving patterns. The narrow depth ranges also suggest the turtles are remaining at a constant depth range and distance from the shore. Most dives are between 10 and 25 m depth. The U dives and 'other' dives show a pattern throughout the day for 21914, with a high proportion of U dives performed between 8 am and 8pm which corresponds to daylight hours in this region (figure 5.17, p. 155). This is opposed to the diving behaviour at Ascension Island where the highest proportion of U dives were performed during the night (see Martin, 2003). An internesting record is not available for individual 21914 to compare U dives directly, but when the U dives are compared with the 3 individuals that provide internesting U dive data, significant differences are seen in the depth and duration ratio for all 3 (ANOVA; $F_{3,429}=29.17$ $p<0.001$; post-hoc tukey test). The duration of the U dives at the coast are significantly shorter than those at Ascension even where there is no significant difference in the depth (figure 5.18, p. 155).

		Depth (m)		Duration (min)	
Dive type	**N**	**Mean±SD**	**Range**	**Mean±SD**	**Range**
Midwater	69	17.61±2.78	11.50-25.00	31.60±7.76	11.94-49.49
Deep	16	39.45±10.55	26.40-57.20	23.73±8.96	8.87-47.50

Table 5.7: Descriptive statistics of 'type 3' midwater dives and 'deep' dives (dives with a maximum depth greater than 25 m) during the approach to Brazil for all turtles combined.

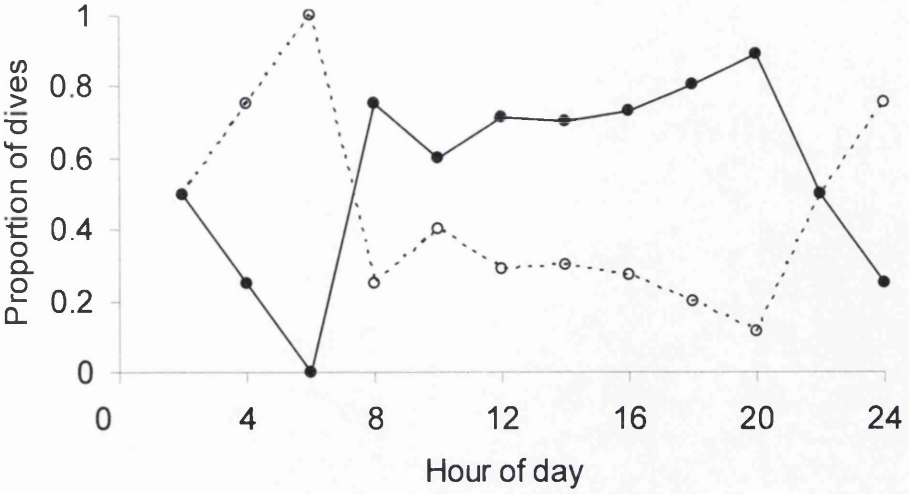


Figure 5.17: The proportion of U dives (●) and non U dives (○) for 2 hour intervals throughout the day during the coastal stage of migration for turtle 21914.

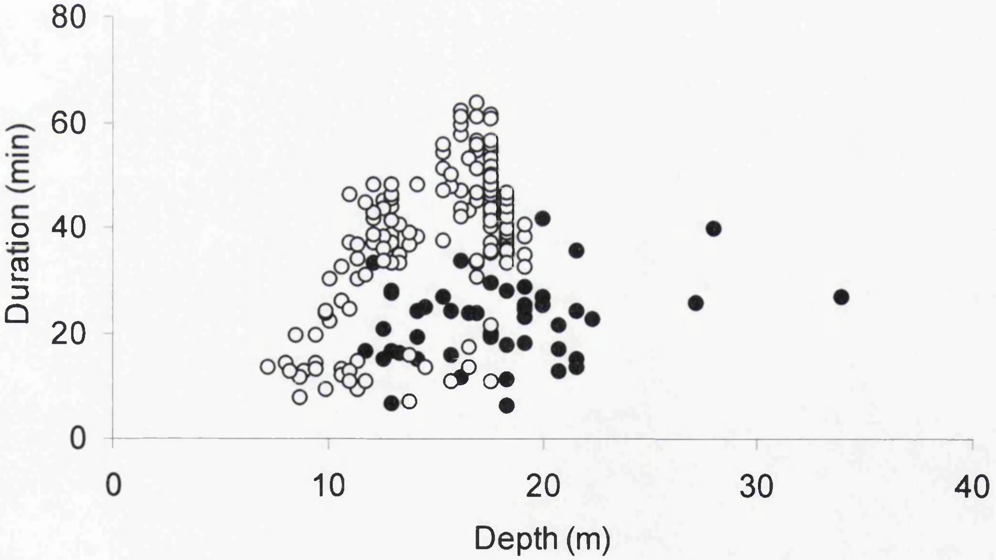


Figure 5.18: The relationship between the depth and duration of U dives for the coastal migration of 21914 (●) and the internesting period of 15119 (○).

5.2.6: Comparison of diving behaviour and speed of travel:

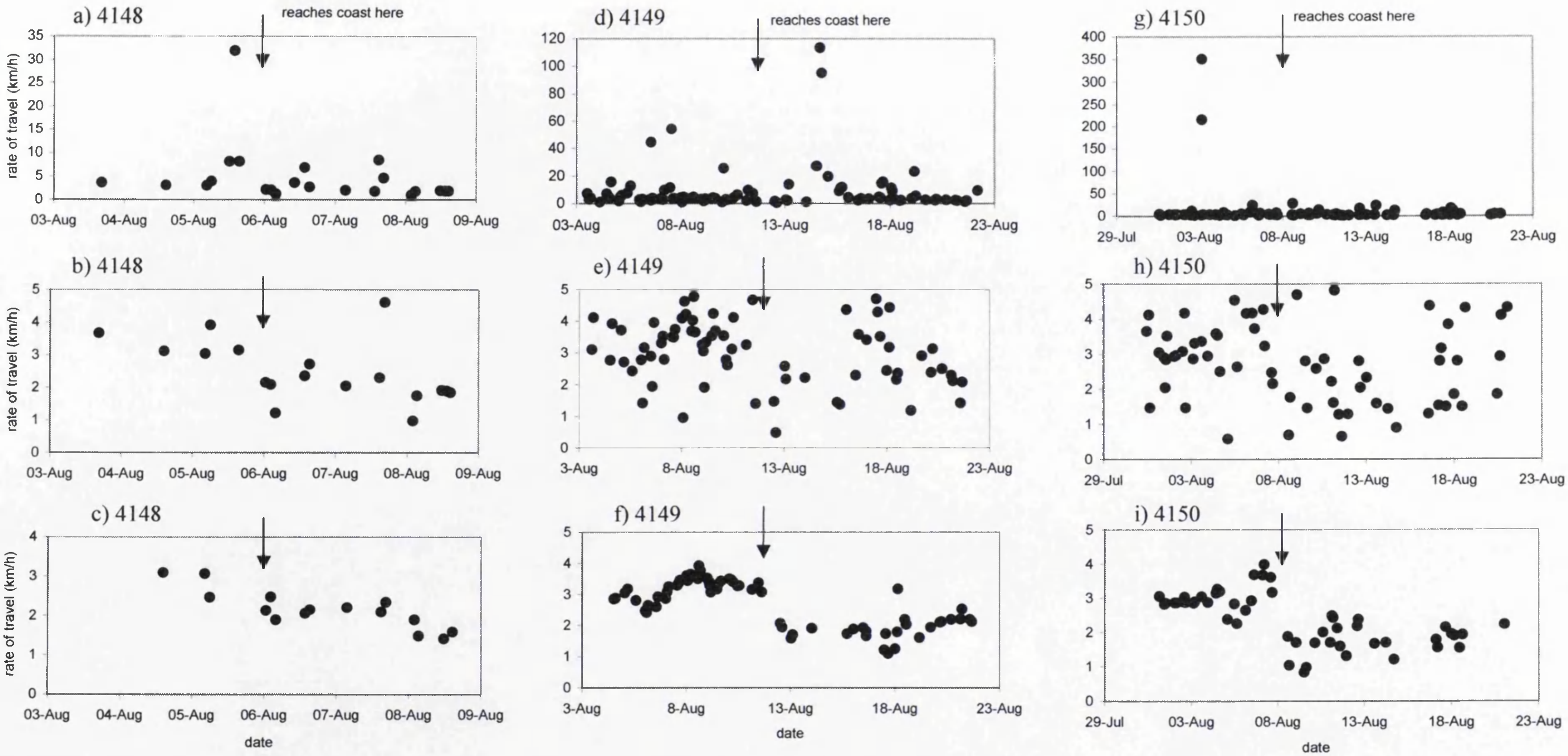
5.2.6.1: Deployment in the Mediterranean Sea:

During post-nesting migration a relatively high proportion of higher accuracy fixes (LC 3, 2, 1) were received (table 5.8, p. 157), as opposed to the Atlantic deployments where the majority of fixes were of LC0, A and B (mean 92% for 11 individuals; see section 4.1 (p. 79) for more details). The mean number of fixes per day was significantly higher for the Mediterranean attachments than those at Ascension (t-test; sea phase $T=-3.96$, $p<0.001$, $DF=28$; coastal phase $T=-4.88$, $p<0.0001$, $DF=49$) (mean±SD for both sea and coast migration; Ascension 2.95±2.62 (n=5 individuals), Cyprus 4.21±1.88 (n=3 individuals)).

When the speed of travel is calculated using all consecutive locations received, there is high variability between the values (range 0.06-351.3km/h) (figure 5.19 a, d, g, p. 158). Discarding points that led to speed values over 5km/h, there is still a high variability of speed during the migration (figure 5.19 b, e, h, p. 158) and little correlation between consecutive speed values (figure 5.20 b, e, h, p. 159). For turtles 4148 and 4149 there appears to be a difference between open sea and coastal speed of travel but this becomes apparent for all three turtles when only locations greater than 12 hours apart are used for calculations (figure 5.19 e, f, I, p. 158). There is high correlation between consecutive speed values (figure 5.20 e, f, i, p. 159) which supports this difference. For all turtles, there is a significant alteration in speed of travel at the point where they reach the coastal waters compared to the open sea crossing (unpaired t-test; turtle 4148, $t_4=2.95$, $p<0.05$; turtle 4149, $t_{42}=12.14$, $p<0.01$; turtle 4150, $t_{43}=9.8$, $p<0.01$), (for descriptive statistics see table 5.9, p. 160).

PTT	Phase	N days	*Location Class*							*Locations per day*	
			3	2	1	0	A	B	Total	Mean±SD	Range
4148	Open sea	2	0 (0)	0 (0)	1 (14)	3 (43)	1 (14)	2 (29)	7	3.0±2.8	1-5
	Coast	2	2 (15)	1 (8)	4 (31)	1 (8)	0 (0)	5 (38)	13	5.0±1.4	4-6
4149	Open sea	9	4 (7)	6 (12)	6 (12)	6 (12)	18 (34)	12 (23)	52	6.1±1.7	4-8
	Coast	11	0 (0)	4 (10)	2 (5)	0 (0)	9 (21)	27 (64)	42	3.5±1.4	1-6
4150	Open sea	8	6 (17)	4 (11)	5 (14)	2 (6)	8 (23)	10 (29)	35	4.8±1.0	3-6
	Coast	13	1 (2)	0 (0)	1 (2)	2 (5)	13 (30)	27 (61)	44	3.2±1.9	0-6

Table 5.8: Performance of satellite transmitters on Mediterranean turtles divided into open sea migration and coastal migration showing the number of fixes received for each location class, and in parentheses, the percentage of each location class. Table also shows the mean number of fixes received per day of migration ± the standard deviation and the range.



a) 4148

b) 4148

c) 4148

d) 4149

e) 4149

f) 4149

g) 4150

h) 4150

i) 4150

Figure 5.19: The effects of filtering on the calculated speed of travel for 4148 (a, b, c), 4149 (d, e, f) and 4150 (g, h, i). The rate of travel has been calculated using all consecutive locations (a, d, g), then consecutive locations after discarding all fixes that would have required a travelling speed of > 5km/h (b, e, h), and then using fixes at least 12 hours apart (c, f, i). Arrows indicate the date when each turtle ceased open sea migration and reached shallow coastal water.

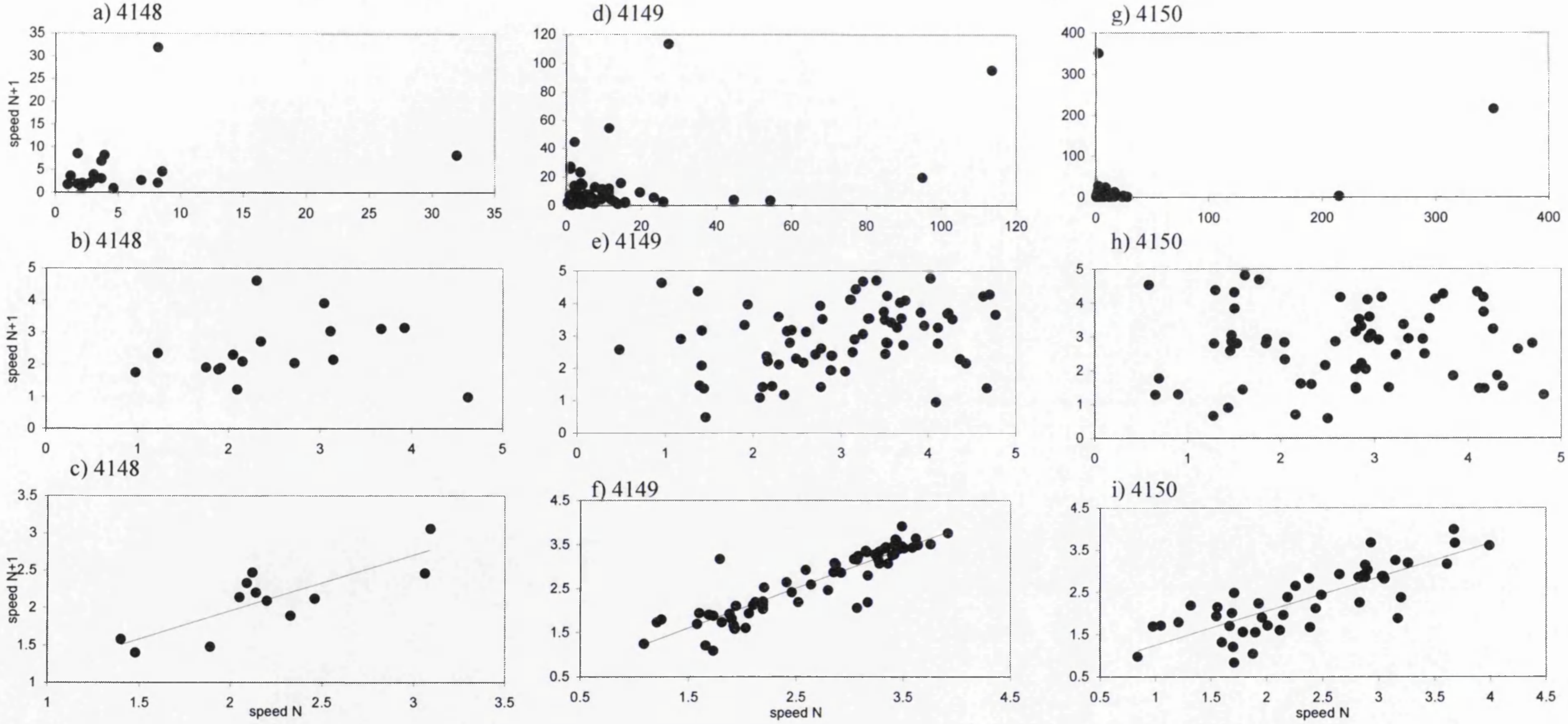


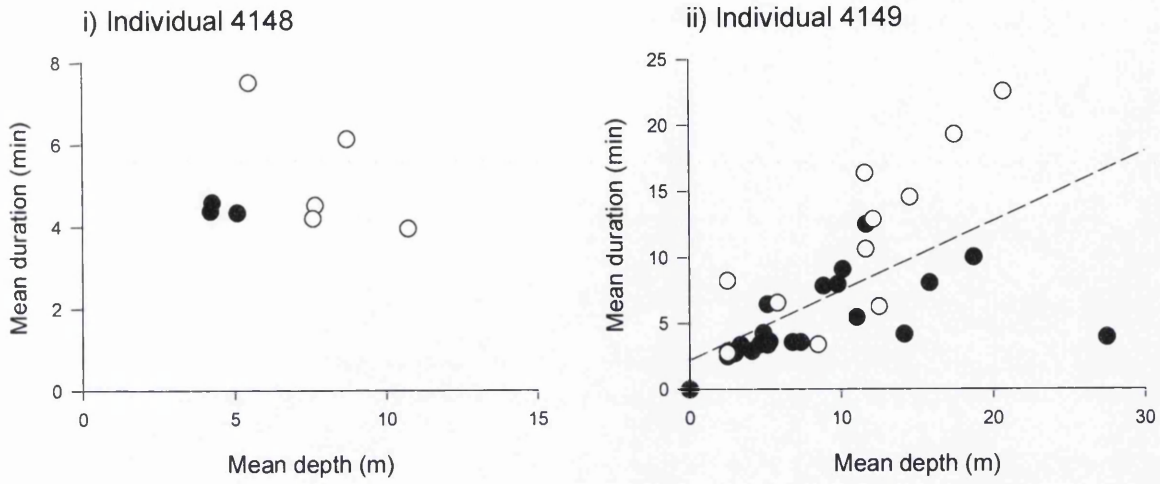
Figure 5.20: Correlation between consecutive speed calculations for 4148 (a, b, c), 4149 (d, e, f) and 4150 (g, h, i), using filters as described in the legend for figure 5.19. (Regression: c: speed(n+1)=0.75speed(n) + 0.456, $F_{1,10}$=20.51, r^2=0.67, p<0.001; f: speed(n+1)=0.903speed(n) + 0.250, $F_{1,62}$=261.46, r^2=0.81, p<0.001; i: speed(n+1)=0.806speed(n) + 0.448, $F_{1,48}$=93.00, r^2=0.66, p<0.001.)

	Phase	**N**	**Mean (kmh^{-1})**	**St.Dev (kmh^{-1})**	**Range (kmh^{-1})**
4148	Sea	4	2.7	0.5	2.1-3.1
	Coast	9	1.9	0.3	1.4-2.3
4149	Sea	36	3.2	0.4	2.4-3.9
	Coast	24	1.9	0.4	1.1-3.2
4150	Sea	23	3.0	0.4	2.3-4.0
	Coast	23	1.8	0.4	0.8-2.5

Table 5.9: Descriptive statistics for the speed of travel using only location fixes of over 12 km apart.

The basic diving behaviour patterns are discussed in Godley et al. (2002).

There is a linear relationship between mean dive depth and mean dive duration for corresponding 6-hour periods during migration for individuals 4149 and 4150 (figure 5.21, p. 162). If these data are divided up in order to compare open sea and coastal diving behaviour, there is a significant difference between mean depth and mean duration between the 2 phases with a predominance of longer, deeper diving along the coast and short, shallow dives during the open sea migration (pooled data for 3 turtles: ANOVA depth $F_{1,73}=11.47$, $p<0.005$; duration $F_{1,73}=18.04$, $p<0.001$). (On an individual level, this difference between open sea and coastal diving behaviour is significant for depth and duration for individual 4150 (ANOVA depth $F_{1,29}=15.22$, $p<0.005$; duration $F_{1,29}=8.63$, $p<0.01$), depth only for 4148 (ANOVA depth $F_{1,6}=9.20$, $p<0.05$) and duration only for 4149 (ANOVA duration $F_{1,34}=12.72$, $p<0.005$)). These data also show a diel pattern. During open sea migration, the mean submergences during 6-hour periods are significantly longer during periods 0 and 1, than periods 2 and 3 for individuals 4149 and 4150 (turtle 4148 - data set too small for individual analysis) (ANOVA; individual 4149 $F_{3,20}=13.09$, $p<0.001$; individual 4150 $F_{3,13}=6.03$, $p<0.01$). As calculating the mean dive duration and depth may over simplify the data set, individual dive variables have been compared. During the open sea migration there is a significant difference in dive behaviour between period 0 and the other 6-hour periods of the day, with a lower proportion of time spent between 0 and 2 m depth and on short dives (<5 min in duration) during the night than any other times of the day for individuals 4149 and 4150 (ANOVA; individual 4149 $F_{3,25}=52.10$, $p<0.001$; individual 4150 $F_{3,15}=44.35$, $p<0.001$, post-hoc Tukey test) (figure 5.23a, p. 163). But then during coastal migration there is no significance between the different



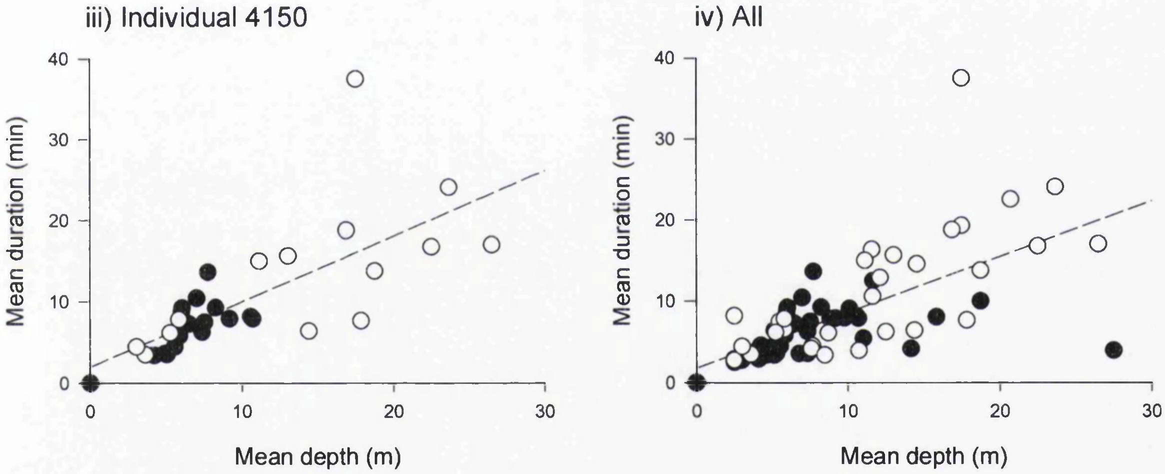
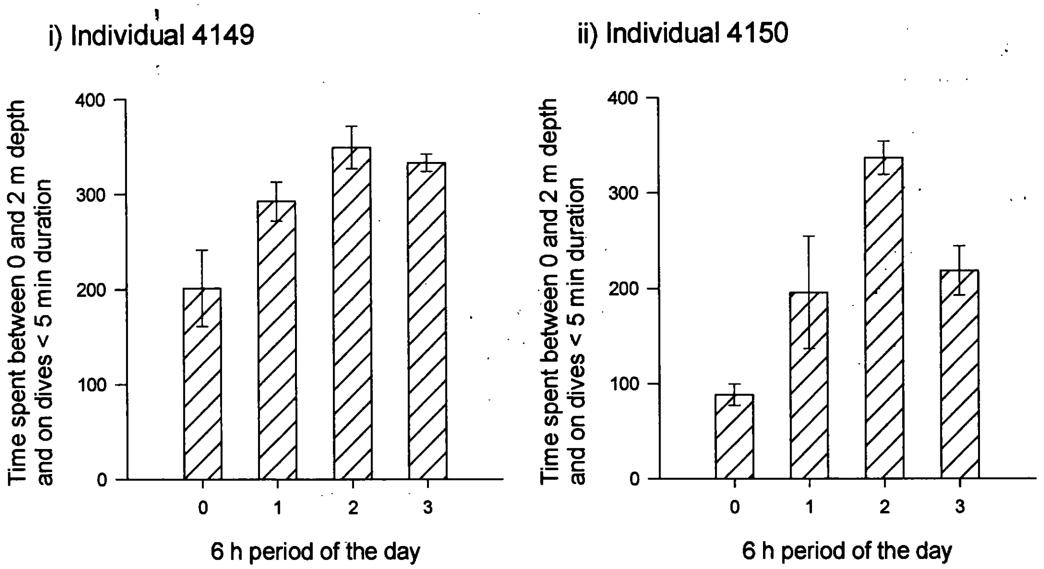


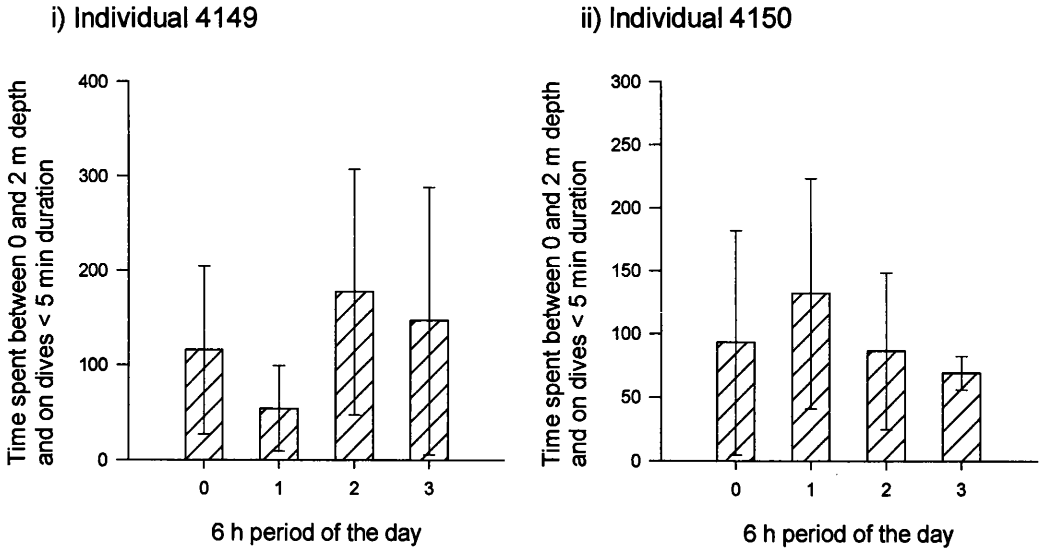
Figure 5.21: Mean dive depth against mean dive duration for corresponding 6-hour periods during migration, for (i) individual 4148, (ii) 4149, (iii) 4150, and iv) data for all turtles pooled. Regression equations: ii) 4149, mean duration = 2.21 + 0.526 depth, $r^2 = 0.40$, $F_{1,\ 34} = 22.57$, $p<0.001$; iii) 4150, mean duration = 1.98 + 0.804 depth, $r^2=0.52$, $F_{1,\ 29}=31.38$, $p<0.001$, and iv) all, mean duration = 1.76 + 0.684 depth, $r^2=0.46$, $F1_{,\ 73}=61.78$, $p<0.01$. In all graphs, data divided into open sea (●) and coastal (○) migration.



i) Individual 4149

ii) Individual 4150

Figure 5.22a: Mean amount of time (+/- 1SD) spent between 0 and 2m and engaged on dives less than 5min duration in the 6hour periods 0, 1, 2 and 3 for all turtles during open sea migration. Periods are in local time (GMT + 3 h); 0 = 21:00-02:59, 1 = 03:00-08:59, 2 = 09:00-14:59 and 3 = 15:00-20:59.



i) Individual 4149

ii) Individual 4150

Figure 5.23b: Mean amount of time (+/- 1SD) spent between 0 and 2m and engaged on dives less than 5min duration in the 6hour periods 0, 1, 2 and 3 for all turtles during coastal migration. Periods as in figure 5.23a.

6-hour periods for either turtle (figure 5.23b, p. 163). Dives longer than 20 min in duration were only recorded during period 0 for all individuals.

When comparing mean speed of travel and diving behaviour between corresponding 6-hour periods, there is not a significant relationship between speed and mean diving depth (all 3 turtles combined; linear regression: $F_{1,30}=1.56$, $p>0.05$, mean depth = 1.11-1.49 mean speed, $r^2=0.05$), but as the speed increases, the mean dive duration decreases significantly (all 3 turtles combined; linear regression: $F_{1,30}= 14.12$, $p<0.05$, mean duration = 15.1-3.09 mean speed, $r^2=0.32$). The proportion of time spent shallower than 2 m and engaged on short dives only shows a significant relationship for individual 4149, but when all data are combined, it increases linearly with mean speed during corresponding 6-hour periods (figure 5.24, p. 165).

Stepwise linear regression was carried out to compare speed of travel with the proportion of dives to different depths and the proportion of time spent engaged on dives of each duration range and between 0 and 2 m. There were inter-individual differences on which variables explained the change in speed. For turtle 4148, 95% of the variation of speed of travel could be explained by the proportion of time spent engaged on short dives between 0 and 5 min alone (linear regression: $F_{1,4}=79.26$, $p<0.01$, $r^2=0.95$, speed of travel = 3.12 - 0.244 1/time 0-5 min) with speed increasing as time on these dives increased (linear regression: speed of travel = 0.52+5.9 time 0-5 min, $F_{1,4}=18.32$, $p<0.05$, $r^2=0.82$). 60% of the variation for speed of travel for 4149 could be explained by the proportion of dives between 5-10 m and the time spent between 0 and 2 m (stepwise linear regression: $r^2=0.60$). The dives between 5 and 10 m explained 48% of the variation alone (linear regression: speed = 2.98+12.2 time 5-

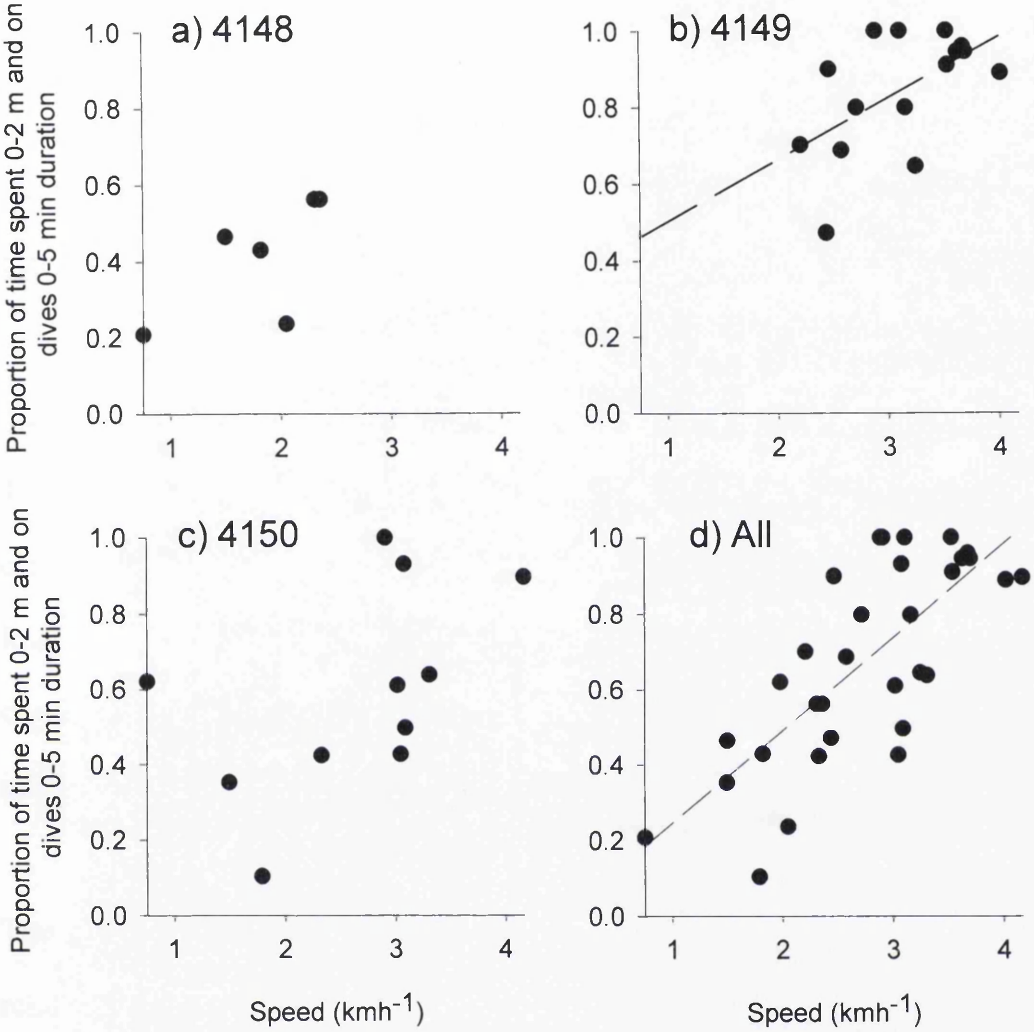


Figure 5.24: The relationship between the proportion of time spent between the surface and 2m depth and on dives less than 5 min long and the mean speed of travel during corresponding 6 hr periods a) 4148, b) 4149 (Linear regression: $F_{1,13}=6.22$, $p<0.05$, mean time 0-2m and 0-5min = 0.341 + 0.16mean speed, $r^2=0.32$), c) 4150 and d) all 3 turtles combined (Linear regression: $F_{1,30}=38.44$, $p<0.05$, mean time 0-2m and 0-5min = 0.246 mean speed, $r^2=0.56$).

10 m, $F_{1,15}=13.81$, $r^2=0.48$, $p<0.01$). Stepwise regression shows that 79% of the variation in speed of travel for 4150 can be explained by the proportion of time between 0 and 2 m and the proportion of dives between 0-5 m and 5-10 m (stepwise linear regression; $r^2=78.6$, $p<0.01$, speed = 1.37 + 1.47(0-5 m) - 5.75 (5-10 m) + 1.45 (0-2 m)), and 43% by the time between 0-2 m only (linear regression: speed = 2.19 + 1.46 time0-2 m, $F_{1,9}=6.68$, $r^2=0.43$, $p<0.05$).

5.2.6.2: Ascension deployment:

The mean speed during the whole oceanic or coastal migration phase does not show a correlation to turtle size (see section 4.2, p. 89). The mean speed was significantly lower during the coastal migration than during the open sea crossing and this was compared to diving behaviour in order to try and identify the factors that most influence travelling speed.

The average dive depth calculated from the 6 hour summary data showed a significant relationship with the overall mean speed of travel (length of entire phase (km)/ duration (h)) for open sea and coastal migration (figure 5.25, p. 167). The depth of the shallow travelling dives during migration is significantly correlated to the overall travelling speed for the oceanic phase, with the speed decreasing as the modal depth of the shallow dives increases ($F_{1,3}=12.18$, $r^2=0.80$, $p<0.05$, (n=5 individuals)). This depth is not significantly related to the CCL of the turtles. The mean speed of travel however does not necessarily reflect the overall patterns of speed as the turtles are seen to vary speed throughout the oceanic phase, travelling faster in some sections and slower in others.

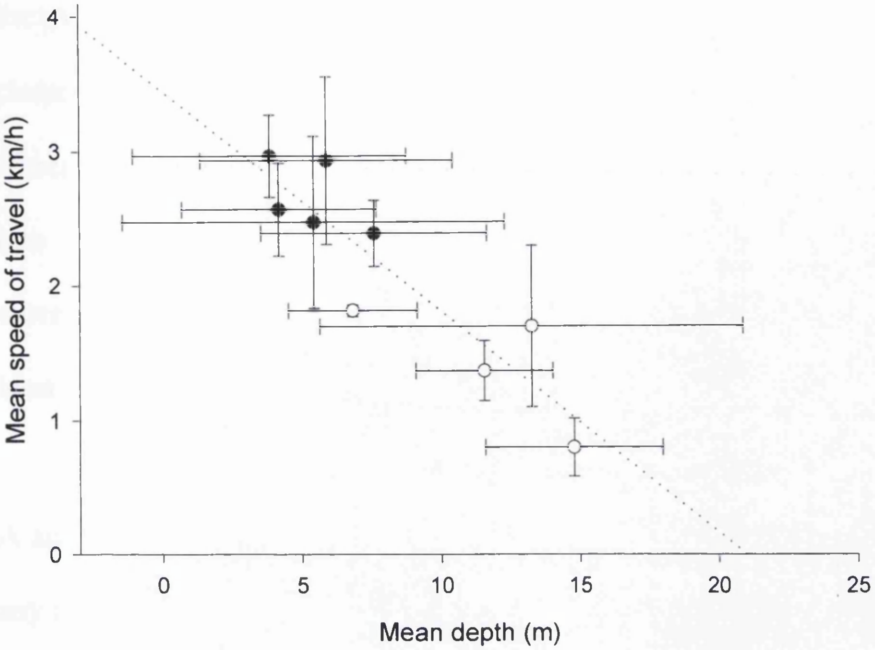


Figure 5.25: Speed of travel compared to average dive depth during migration for 5 individuals (horizontal error bars, ± 1SD) (Linear regression, speed = 3.62-0.180 depth; r^2=0.91, $F_{1,6}$=62.34, $p<0.001$). Data points shown as open sea (●) and coastal migration (○) (no coastal data for individual 15121).

During the Mediterranean deployments, many more fixes were received per day than the Ascension deployments and a higher proportion were of the higher accuracy classes. This allowed 6 hour diving periods to be compared with speed of travel. The Ascension transmitters, however, provided fewer fixes and hence the data were split into 2 day means so that speed of travel and dive behaviour could be compared in more detail. (By using two day means, the fixes used for speed calculations were at least 87km apart.)

A spreadsheet was created containing the following parameters in order to identify any relationships between them during the open sea migration; the variables included were: turtle size, speed of travel, speed and direction of ocean current, direction of the turtle compared to the ocean current, the mean depth (from 6hour summaries), the time deep (from 6hour summaries), the number of shallow dives and deep dives recorded in a 6 hour period, the mean depth and duration of the dive profiles, the mean depth of midwater dives, the mean duration of midwater dives, the proportion of time engaged on midwater diving and conducting 'other' shaped dives, mean depth of shallow dives and day of migration (inputed as a percentage of total journey time). Step-wise regression was carried out to investigate the influence of potential factors on the speed of travel of the migrating turtles and no significant relationships were found. (The speed of travel was however found to be related to the distance and time between the 2 fixes used for the speed calculation (regression analysis: speed = 1.54 + 0.0114 distance between fixes, $F_{1,53}=12.83$, $r^2=0.20$, $p=0.001$; speed = 4.43-0.0396time, $F_{1,53}=21.21$, $r^2=0.29$, $p<0.001$.)) The average depth of the type 3 midwater dives does appear to decrease as speed increases, although this is not a statistically significant relationship (figure 5.26, p. 169). The mean depth and duration

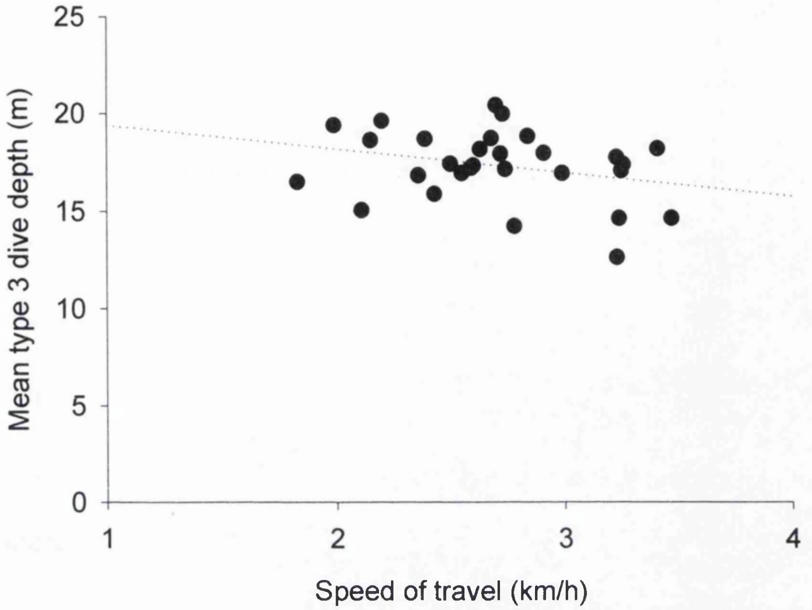


Figure 5.26: The relationship between speed of travel and mean depth of the type 3 dives in corresponding 2 day periods during migration (regression analysis: mean depth=20.6-1.23speed, $F_{1,27}=2.56$, $r^2=0.09$, $p=0.121$).

of the type 3 dives is significantly related in two day means (figure 5.27, p. 171). The number of shallow dives recorded during a 6hour period was related to the day of migration; this decreased significantly over time (figure 5.28, p. 172). It followed that the mean time spent on engaged on deep diving increased over time (regression, time deep=20.2+0.822day of migration, $F_{1,42}=9.09$, $r^2=0.18$, $p<0.005$). The number of deep dives is highly significantly related to the time spent on deep diving (regression: number of deep dives=0.192+0.157 time deep, $F_{1,42}=173.72$, $r^2=0.80$, $p<0.001$). The number of deep dives recorded also drops significantly as the mean duration of each increases (regression: number of deep dives=10.2+0.190 mean dive duration (min), $F_{1,42}=10.3$, $r^2=0.20$, $p<0.005$).

No significant relationships are seen between speed of travel and dive behaviour in 2 day means at the individual level either. However, the two larger turtles (15119 and 15122) spend a significantly higher proportion of time engaged on type 3 dives than the two smaller individuals (t-test; T=6.30, $p<0.0001$, DF=48) and these dives are significantly longer (t-test; T=2.38, $p<0.05$, DF=27).

5.3. Diving behaviour at the residence areas:

Of the 7 transmitters attached to nesting green turtles on Ascension Island, 4 continued to transmit data for up to 58 days after the turtles had completed their post-nesting migration and ceased movement in the coastal waters off Brazil.

Although the number of dive summaries received is low, the percentage of time spent engaged on dives greater than 6m in depth and the average dive depth reflects the

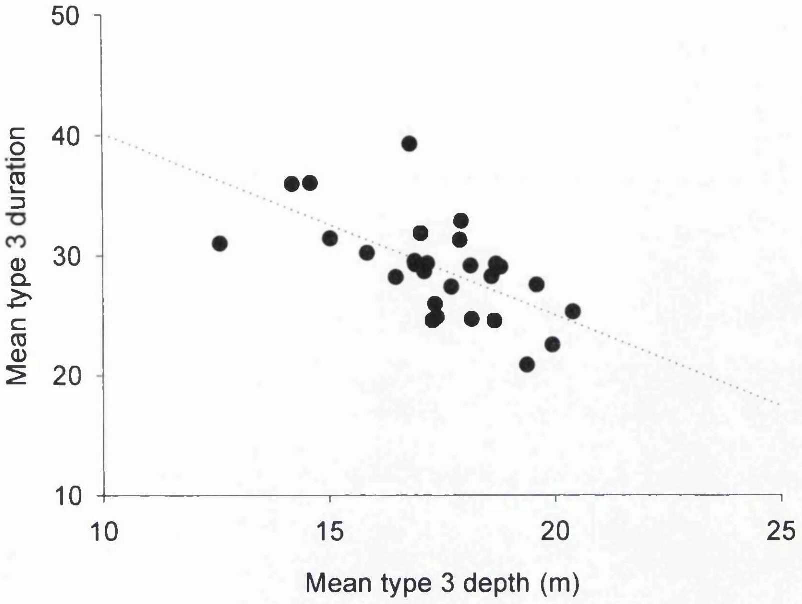


Figure 5.27: The relationship between depth and duration of type 3 dives in two day means (regression analysis: duration=55.3-1.52depth, $F_{1,27}=19.13$, $r^2=0.42$, $p<0.001$).

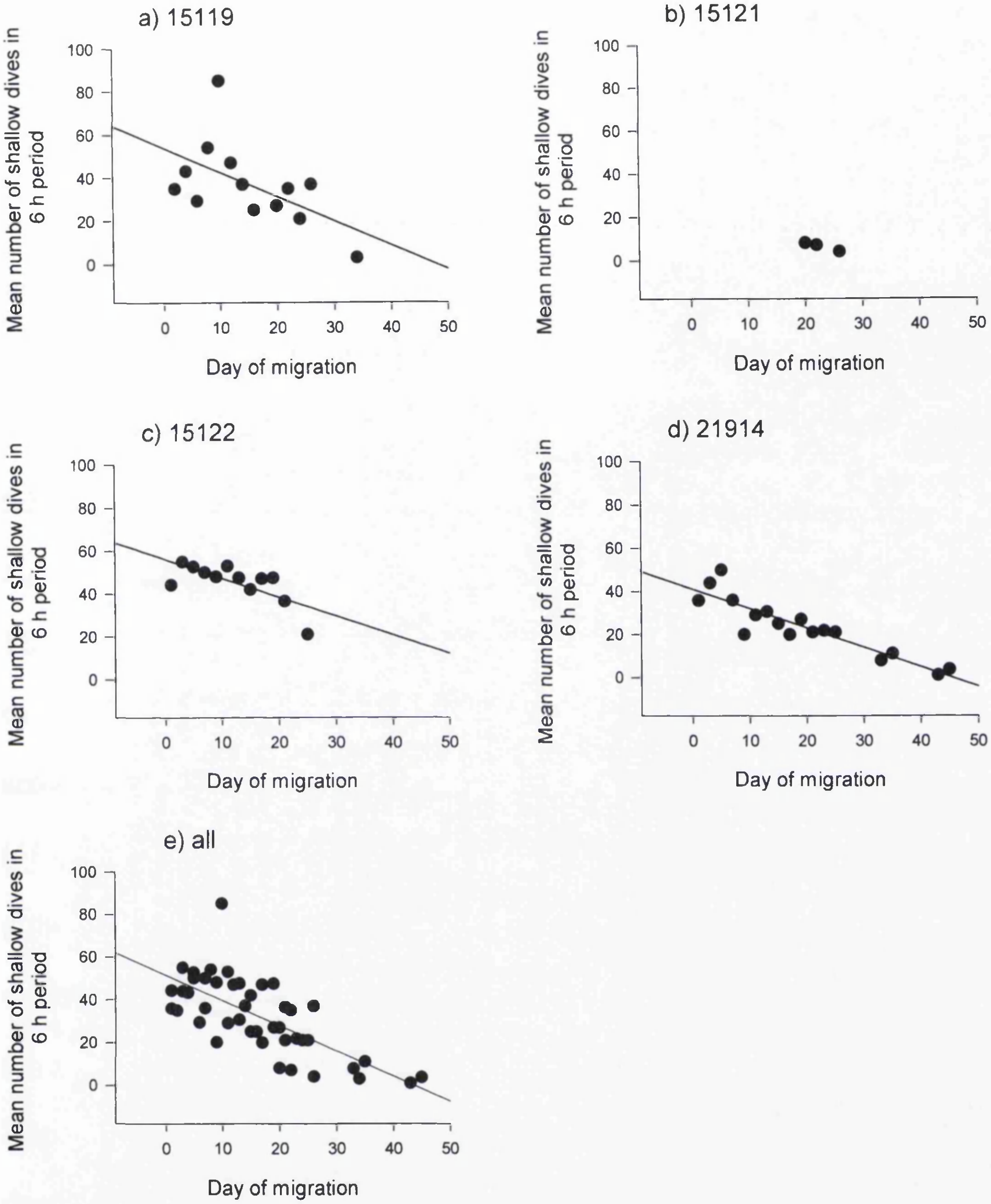


Figure 5.28: The relationship between the mean number of shallow dives (dives less than 6m in depth) during a 6 h period and the day of migration for 4 individuals (a-d) and for all data combined (e). Regression equations a) shallow dives (n) = 53.9-1.12 day of migration, $F_{1,11}$=4.94, r^2=0.31, $p<0.05$; c) shallow dives (n) = 56.1-0.881 day of migration, $F_{1,10}$=10.70, r^2=0.52, $p<0.01$; d) shallow dives (n) = 41.1-0.905 day of migration, $F_{1,15}$=72.42, r^2=0.83, $p<0.001$; e) shallow dives (n) = 51.5-1.18 day of migration, $F_{1,43}$=45.5, r^2=0.51, $p<0.001$.

depth selections seen from the bathymetry with turtles in shallow water habitats spending a relatively low proportion of time on dives to a depth greater than 6m (table 5.11, p. 174). The median dive profile duration and maximum depth also shows a dichotomy between the turtles with short shallow diving dominating the behaviour of two of the turtles, whilst the other two engage in longer deeper dives (table 5.12, p. 174).

5.3.1: Diel patterns in submergence behaviour:

5.3.1.1: Mediterranean turtles:

The transmitters attached to the Mediterranean turtles worked for 282, 243 and 267 days at the foraging grounds (turtles 4148, 4149 and 4150 respectively), lasting from arrival after the post-nesting migration, throughout the winter and for two turtles (4148 and 4150), into the next spring. When the turtles first arrived at the foraging grounds the behaviour was dominated by short and shallow dives, with a significant diel pattern to the diving behaviour during the autumn months (figures 5.29a, b and c, pp. 175-176) (see appendix for descriptive statistics). The time spent conducting dives less than 10min in duration was significantly less at night (period 0) than during the daytime (period 2) (t-test; turtle 4148; T_{51}= -10.28, p<0.01; turtle 4149; T_{46}= -2.76, p<0.01; turtle 4150; T_{43}= -6.13, p<0.01), hence mean dive duration was significantly greater at night (t-test; turtle 4148; T_{51}= 8.91, p<0.01; turtle 4149; T_{22}= 4.29, p<0.01; turtle 4150; T_{28}= 5.87, p<0.01) and consequently the number of dives recorded was less. For turtle 4148, the mean dive depth was significantly greater at night, whilst there was no such significant diel pattern in depth for turtles 4149 and 4150 (t-test; turtle 4148; T_{50}= 3.54, p<0.01; turtle 4149; T_{44}= -0.11, p=0.91; turtle 4150; *All values identical*).

Individual	N	Average depth (m)	Average % time deep	Bathymetry (m)
15119	20	4.37	23.31	3
15122	34	4.24	25.95	2
21914	10	23.76	80.72	35
4394A	4	14.94	89.04	17

Table 5.11: Mean values for the depth and the percentage of time deep (>6m) at the foraging grounds calculated from the 6hour summary results. Also shown is the depth taken from bathymetry charts at the mean position of each individual.

Individual	N	Median duration (min)	IQ range	Median max depth (m)	IQ range
15119	82	6.7	4.2-13.9	8	6.9-8.9
15122	123	14.9	6.5-25.4	9.3	8.1-10.3
21914	94	25.1	19.0-38.5	28.8	22.2-30.8
4394A	26	32.9	19.0-44.9	20	14.2-21.8

Table 5.12: Median dive duration and depth (and inter-quartile ranges: IQ) using dive profiles from the foraging phase. Profiles that include zero depth readings have been excluded from this analysis.

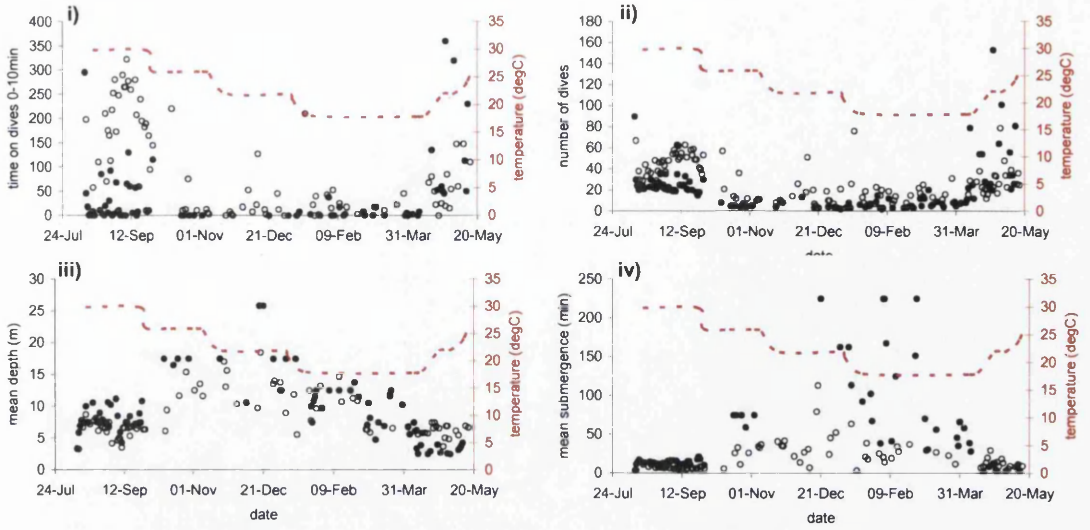


Figure 5.29a: The dive behaviour of turtle 4148 during night (●=period 0) and daytime (○=period 2). Graphs show for each 6 hour period, i) the time spent engaged on dives less than 10min in duration, ii) the number of dives conducted, iii) the mean depth of dives, and iv) the mean dive duration.

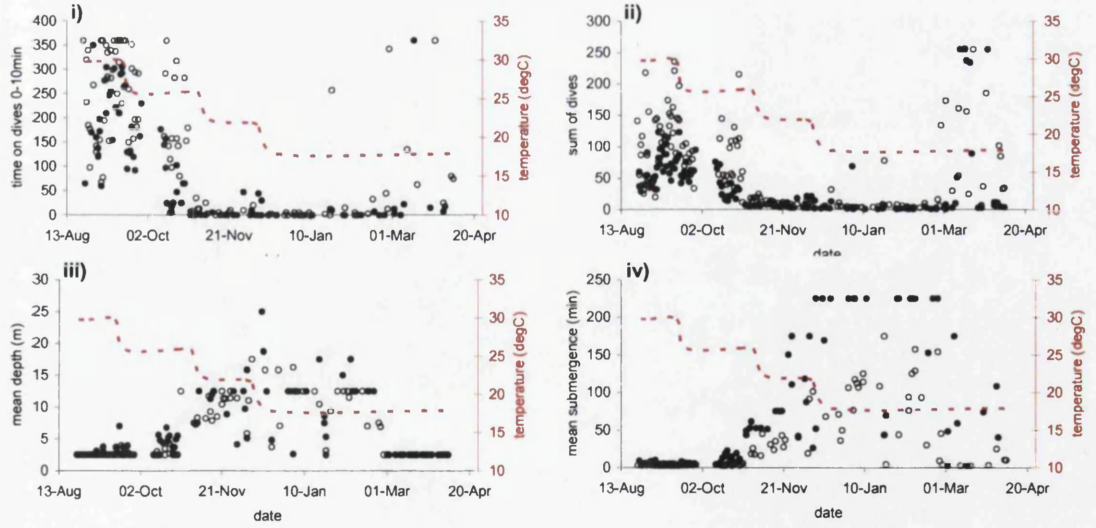


Figure 5.29b: The dive behaviour of turtle 4149 during night (●=period 0) and daytime (○=period 2). Graphs show for each 6 hour period, i) the time spent engaged on dives less than 10min in duration, ii) the number of dives conducted, iii) the mean depth of dives, and iv) the mean dive duration.

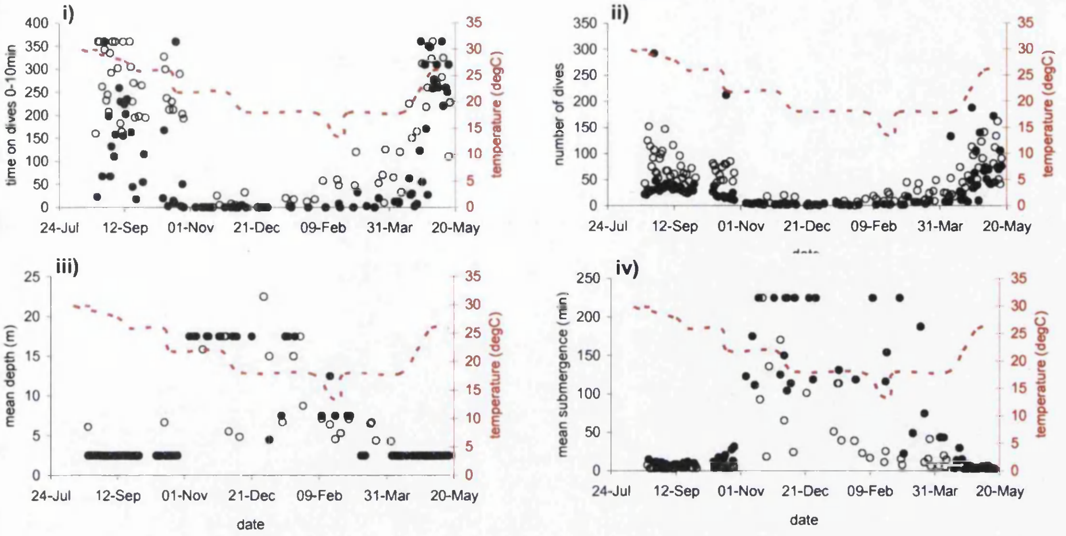


Figure 5.29c: The dive behaviour of turtle 4150 during night (●=period 0) and daytime (○=period 2). Graphs show for each 6 hour period, i) the time spent engaged on dives less than 10min in duration, ii) the number of dives conducted, iii) the mean depth of dives, and iv) the mean dive duration.

During the winter months, the submergence time was high for all turtles. The diel patterns varied between the turtles over-winter. There was no significant day/night difference that could be noted between the mean dive depth for all individuals (t-test; turtle 4148; T_{62}= 1.15, p=0.26; turtle 4149; T_{28}= 1.20, p=0.24; turtle 4150; T_{39}= 0.79, p=0.43). For turtle 4148, the time spent engaged on short dives was significantly higher during the day (t-test; T_{38}= -3.22, p<0.01) and hence, the mean submergence time lower (t-test; T_{33}= 5.41, p<0.01). For turtle 4149, there were no significant differences between the time spent engaged on dives less than 10min in duration when comparing night with day (t-test; T_{19}= -1.52, p=0.15), but there was a significant difference in the mean dive duration (t-test; T_{34}= 4.87, p<0.01). For turtle 4150, significantly more time was spent on shorter dives and mean dive duration was lower during the daytime compared to the night (t-test; time on dives<10min T_{25}= -3.73, p<0.01; mean duration; T_{45}= 4.66, p<0.01).

The transmitters continued to work into the next spring for 2 of the turtles (4148 and 4150). No diel patterns were seen with both turtles spending a high proportion of time engaged on dives less than 10min long. In fact for turtle 4150, 77% of the time was spent on dives less than 10min long or between the surface and 2m depth. The behaviour seen during the periods that included dawn and dusk (1 (3:00-08:59) and 3 (15:00 to 20:59)) varied between the turtles and between the seasons.

In the autumn, there was no significant difference in the diving behaviour seen during periods 2 (daytime) and 3 (dusk) for turtle 4148 (t-test; time on dives <10min, T_{47}= 0.87, p=0.39; mean duration, T_{47}= -1.92, p=0.06). During the winter period 1 was closely correlated to period 0 with no significant difference in mean dive duration (t-test; T_{60}= -0.98, p =0.33) or the time spent engaged on short dives (t-test; T_{60}= 0.61, p = 0.54). For turtle 4149, the behaviour was very similar between periods 0 and 1, and also between periods 2 and 3. In the autumn, the number of submergences was not significantly different between periods 0 and 1 (t-test; T_{63}= -1.19, p=0.24) and between periods 2 and 3 (t-test; T_{73}= -0.83, p=0.41). Periods 0 and 1 did not have a significantly different value for the time spent on short dives or the mean dive duration (t-test; time on dives<10min, T_{43}= -0.83, p=0.41; mean duration, T_{36}= -1.14, p=0.26) whilst the relationship between periods 2 and 3 was variable. The mean submergence time was not significantly different in the autumn (t-test; T_{59}= -0.80, p=0.43) whilst the time spent on short dives showed some difference (t-test; T_{59}= -2.63, p=0.01). Over winter no significant difference was seen in the time spent on dives less than 10min duration (t-test; time on dives <10min, T_{20}= 1.1, p=0.28; mean duration, T_{35}= -2.64, p=0.01). For turtle 4150, in the autumn the time spent on dives less than 10min in duration was not significantly different between 0 and 1, (t-test; T_{39}= -0.81, p =0.43) and then 2 and 3 (t-test; T_{63}= 0.18, p =0.86), whilst during the winter the behaviour during these periods was variable.

5.3.1.2: Ascension Island turtles:

The dive summaries can provide an indication of any diel behaviour patterns. Fixes are not really accurate enough to describe any movements within the foraging areas with respect to temporal patterns over the period of the study or any diurnal movements but the 6 hour summaries can show any overall changes in behaviour throughout the 24 hour cycle. This is especially useful where there is a paucity of dive profile data due to the shallow water habitat selection by individuals 15119 and 15122.

There appears to be diel patterns for the turtles that selected shallow water habitats (15119 and 15122) as opposed to those that were in deeper water (21914 and 4394A) (figure 5.30, p. 180) although the difference in diving behaviour between day (periods 2 and 3) and night (periods 0 and 1) was only significant for individual 15122 (t-test: average % time deep, $T_{22}=3.37$, $p<0.05$; average depth (m), $T_{24}=3.4$, $p<0.01$). For turtle 15119, it appears that dives during the day are short and shallow, whereas at night they are longer in duration and to a greater depth but the difference is not significant perhaps due to the low number of dives recorded.

15119 and 15122 remained in very shallow water and hence dive profiles cannot be examined in detail. During the whole period at the foraging areas the deepest dives recorded are 11.8m for 15119 and 12.6m for 15122. 91% (n=75) and 81% (n=100) of dive profiles received for individuals 15119 and 15122 respectively contain at least one zero depth value. However, overall behavioural patterns from the individual dive records show a significant difference between the mean depth and duration of dives during the day and night (figure 5.31, p. 181, and figure 5.32, p. 182). Shallow dives (<6m) dominate daytime behaviour and profiles are recorded more during the night, hence dives are significantly shorter and shallower during the day than at night (t-test; 15119: depth $T_{134}=6.52$, $p<0.0001$; duration $T_{188}=4.90$, $p<0.0001$; 15122: depth $T_{212}=10.77$, $p<0.0001$; duration $T_{212}=6.23$, $p<0.0001$). Of the 22 U dives that could be identified for individual 15122, only 6 were performed between sunrise and sunset.

Although turtle 4394A was resident in deeper water off the coast of Brazil, the transmitter performed poorly and hence only a few profiles were recorded. Only

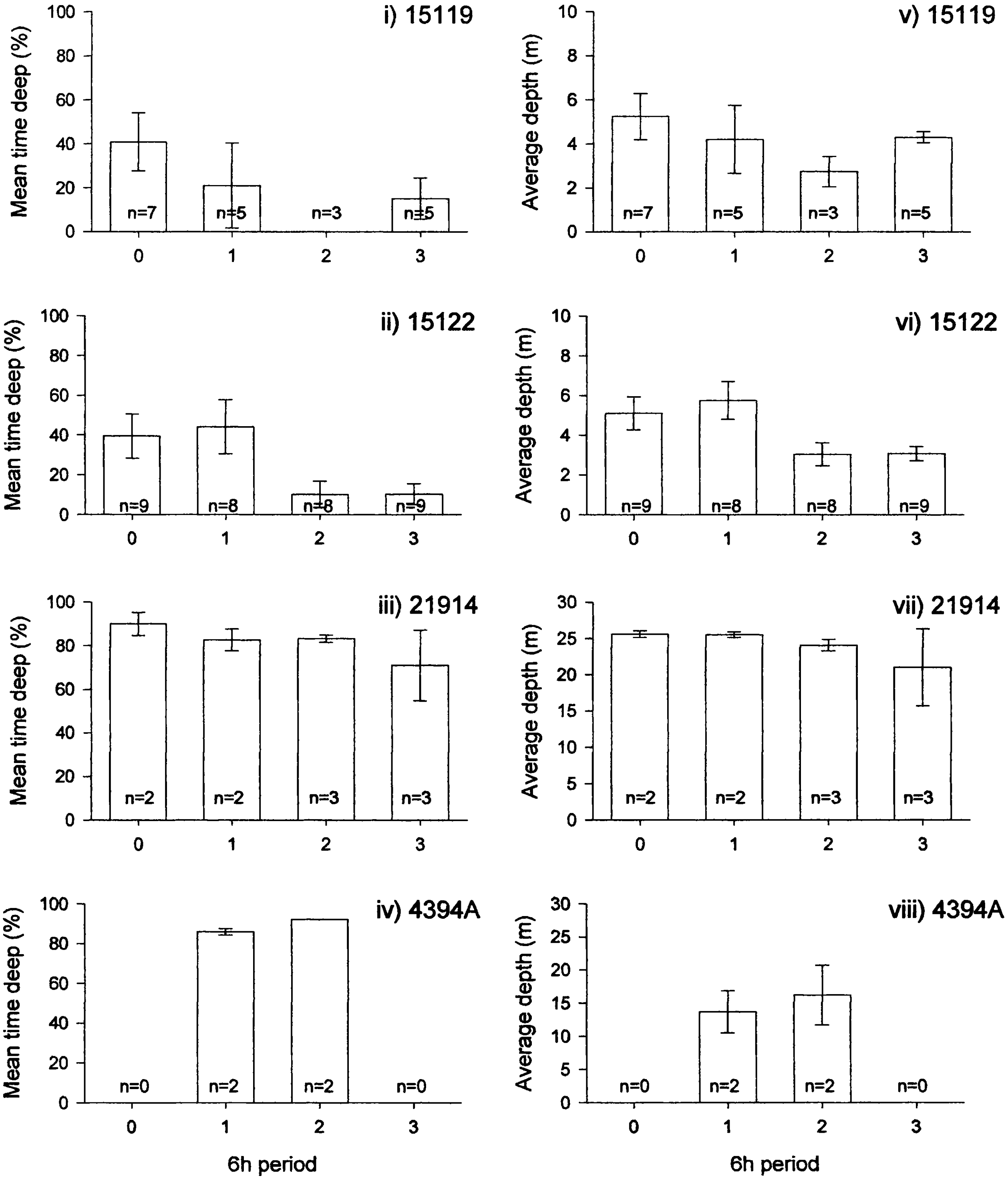


Figure 5.30: The mean time engaged on dives greater than 6m in depth (i, ii, iii and iv) and the average depth (v, vi, vii and viii) recorded for the 6hour periods of the day during time spent at the foraging grounds.

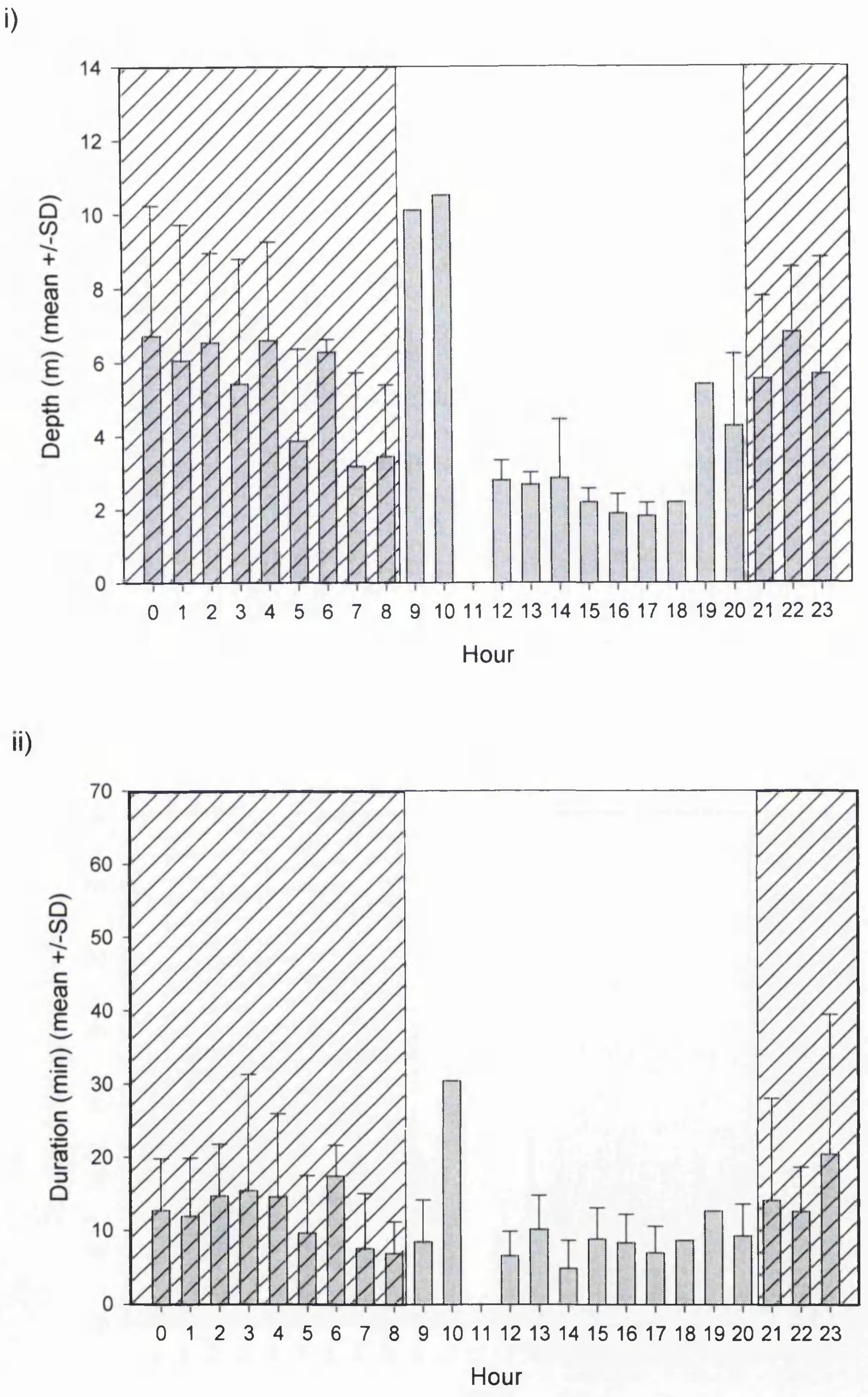


Figure 5.31: The distribution of i) depth and ii) duration of individual dives for 15119 throughout the 24hour cycle at the foraging grounds. Bars show mean value +/- SD. Shaded areas indicate night-time hours between sunset and sunrise. Data includes all dive profiles (n=82) and shallow dives (n=136).

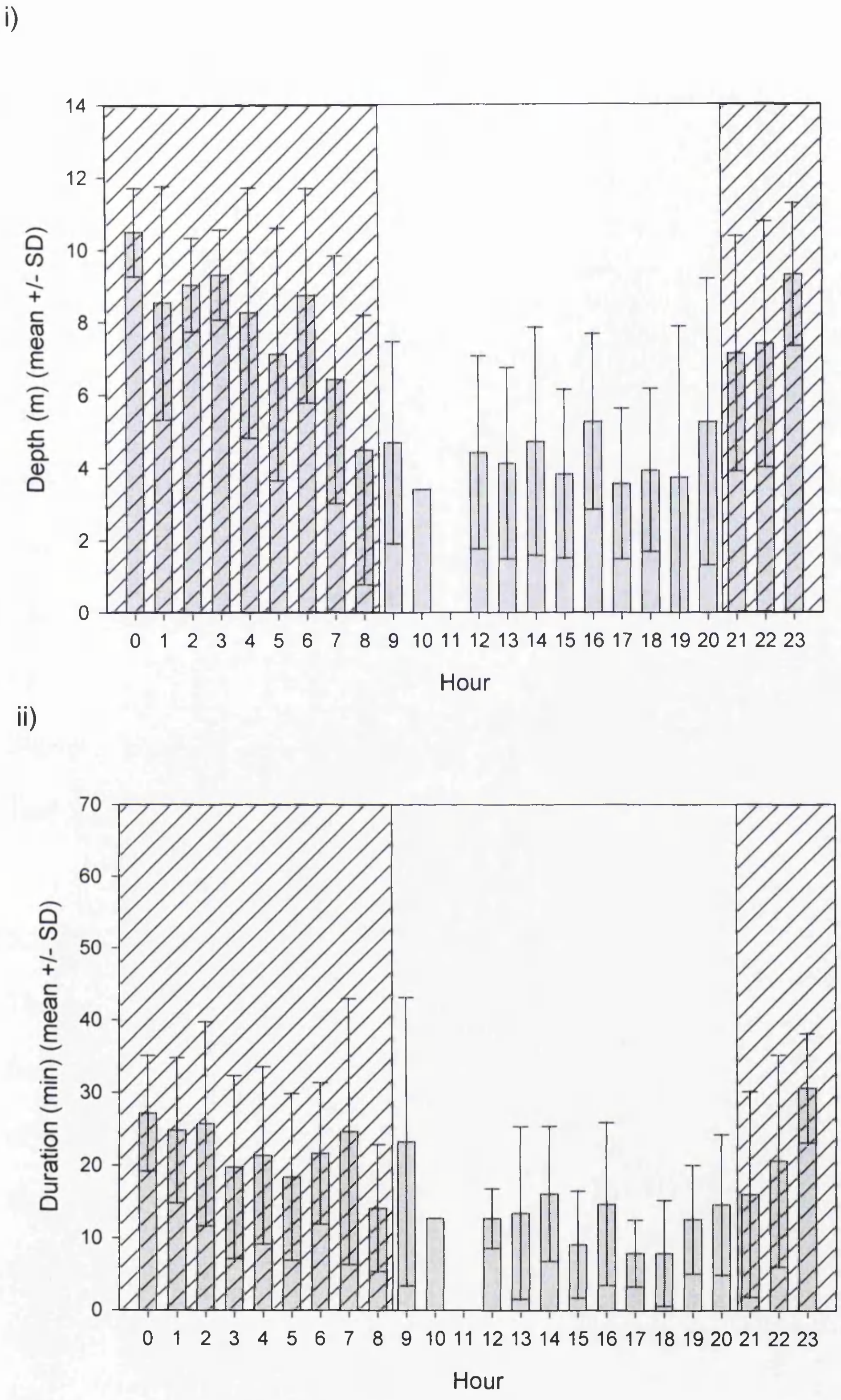


Figure 5.32: The distribution of i) depth and ii) duration of individual dives for 15122 throughout the 24hour cycle at the foraging grounds. Bars show mean value +/- SD. Shaded areas indicate night-time hours between sunset and sunrise. Data includes all dive profiles (n=123) and shallow dives (n=118).

21914 provided a data set of sufficient quantity to examine dive types at the foraging ground in more detail. The majority of dive profiles recorded were U-shaped dives and these were more frequent during the night (figure 5.33, p. 184). There is no significant day/night difference in mean dive depth for these U-dives (figure 5.34i, p. 185), but duration is significantly shorter during daylight hours than at night (figure 5.34ii, p. 185) (t-test: $T_{50}=2.99$, $p<0.005$). If the depth/duration relationship is indicative of the activity level during a dive, then there appear to be peaks of activity mid-morning, mid-afternoon and around dusk (figure 5.35, p. 186). The percentage of dive spent on the 'bottom time' is proportional to the depth/duration relationship, both parameters which are used to define U(a) and U(b) dives. The depth/duration ratio is significantly greater and the bottom time significantly lower during the daytime (figure 5.36, p. 186) (t-test: depth/duration, $T_{52}=-3.92$, $p<0.0005$; bottom time, $T_{62}=3.38$, $p<0.005$) implying U(b) dives during the daytime and U(a) at night.

5.3.2: Comparing U-dives at foraging grounds and Ascension Island:

The U(a) resting dives of 15122 at Ascension clearly fit with regression lines taken from a previous study on internesting green turtles (figure 5.37, p. 187). The majority of the U(b) dives for 15119 at Ascension are below these regression lines. Although the U(a) dives for 21914 at the foraging area are significantly longer than the U(b) dives (duration; t-test $T_{50}=-5.06$, $p<0.0001$), they are still significantly shorter compared to their depth than internesting dives (depth/duration; t-test $T_{36}=13.55$, $p<0.0001$).

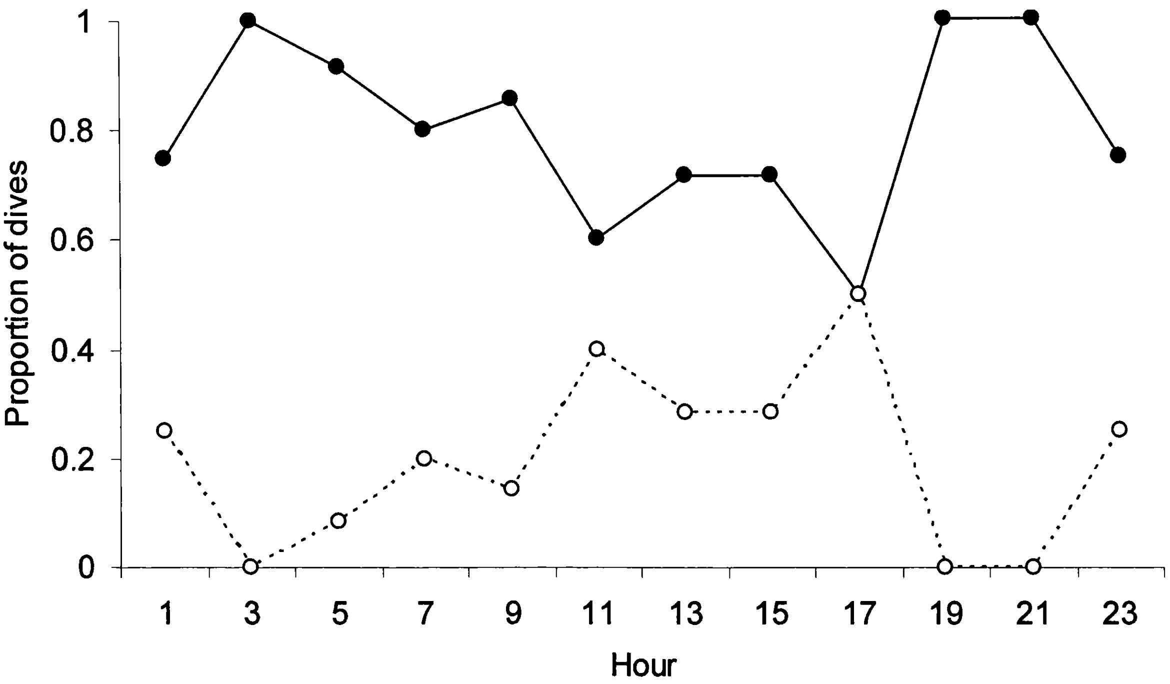


Figure 5.33: The proportion of U-dives (closed circles) and non-U dives (open circles) in 2 hour intervals throughout the 24hour cycle for 21914 at the foraging area.

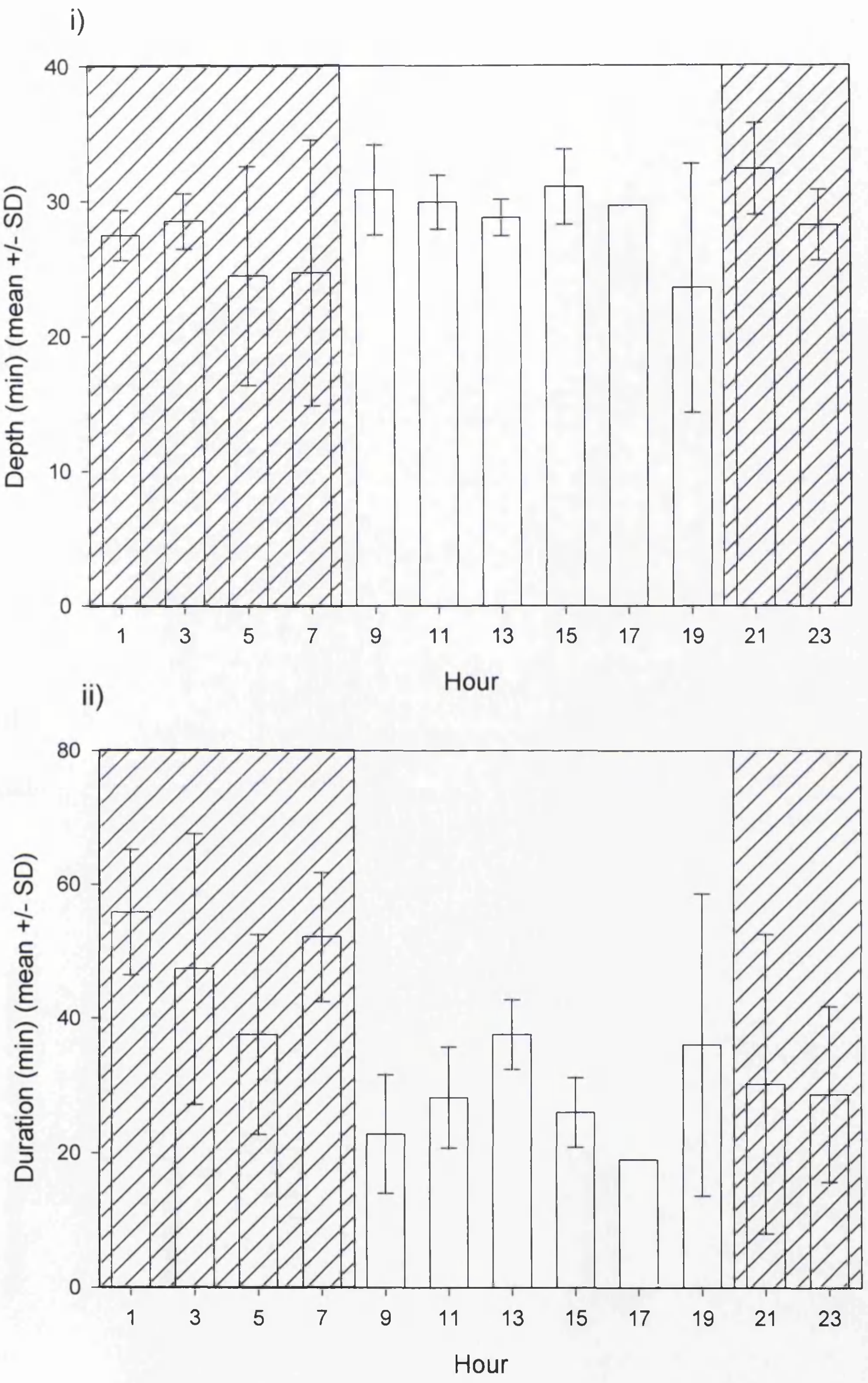


Figure 5.34: For 21914, the mean depth (i) and duration (ii) (+/-SD) of U dives in 2 hour intervals throughout the 24 hour cycle at the foraging ground. Shaded areas indicate night-time.

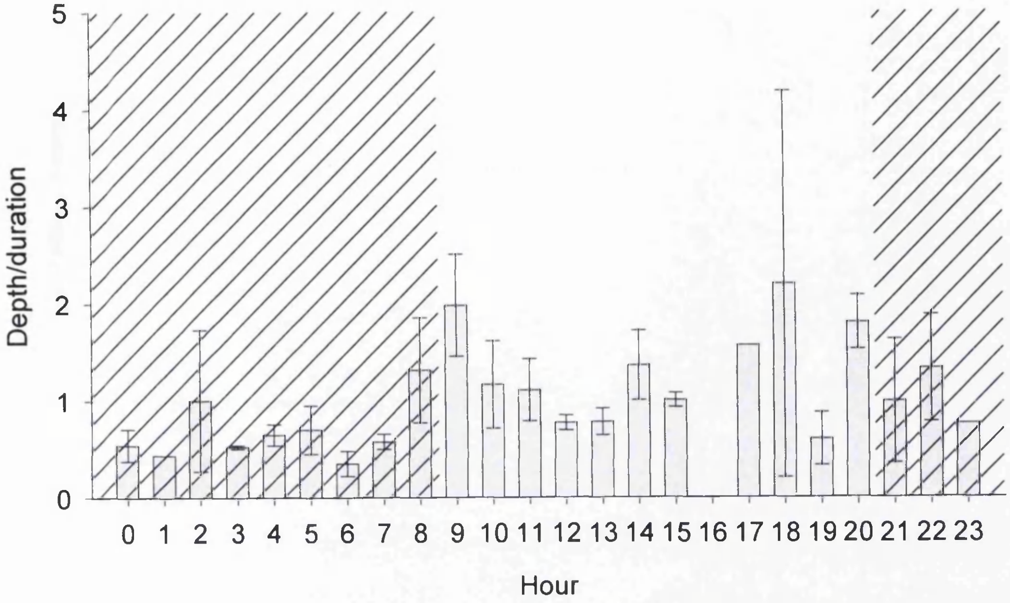


Figure 5.35: The depth/duration ratio for hourly intervals during the day for U-dives of 21914. Each bar represents the mean value with error bars of 1SD. (Shaded areas indicate night time.)

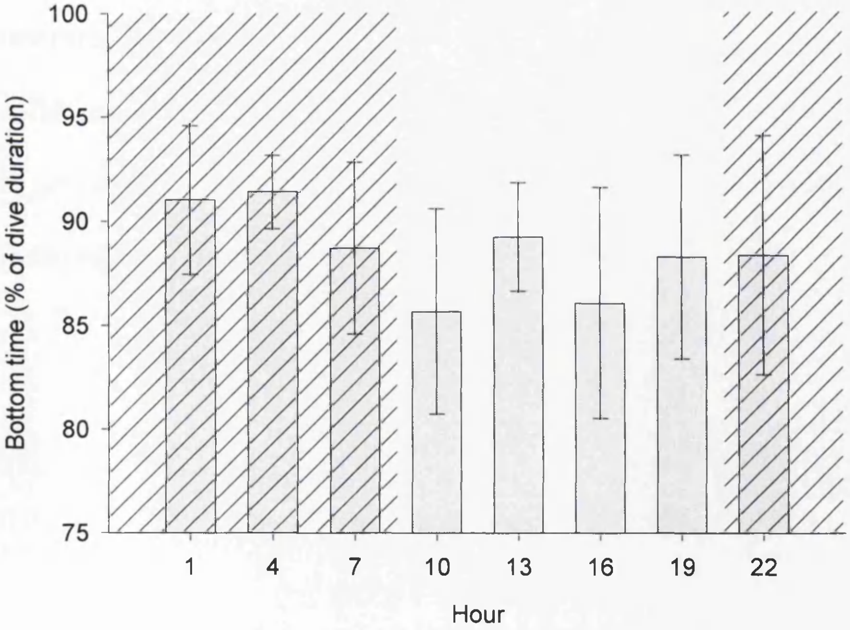


Figure 5.36: The mean bottom time (as % of dive duration) (+/-SD) in 3 hour intervals throughout the 24hour cycle for the U-dives recorded for 21914. (Shaded areas indicate night time.)

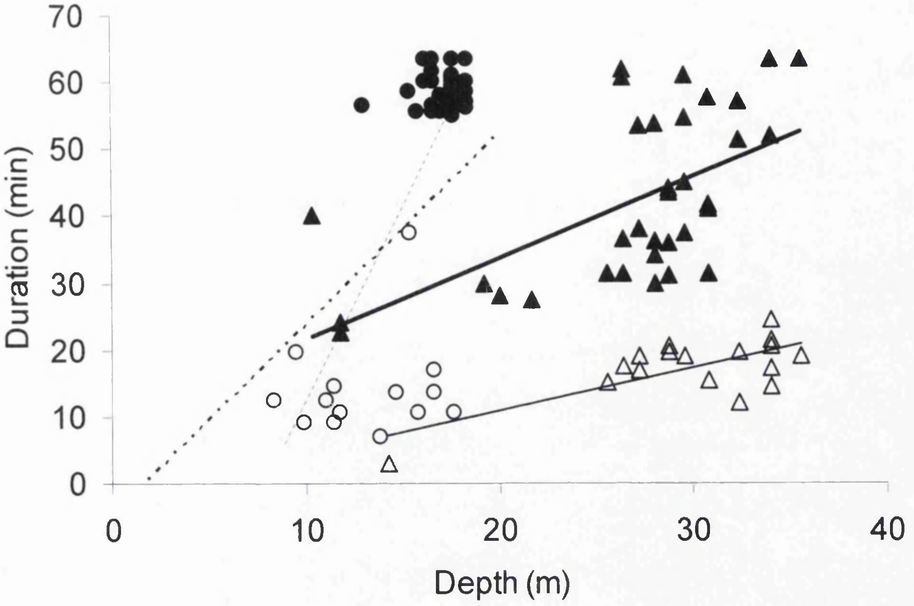


Figure 5.37: The relationship between dive depth and duration for U-dives performed at Ascension by 15119 (○) and 15122 (●) and at the foraging ground by 21914 (Δ and ▲). Closed symbols indicate U(a) dives and open symbols U(b). Dashed regression lines shown are from Hays et al. (2000a) from resting dives provided by TDRs on an internesting green turtle at Ascension Island, whilst the solid lines are for 21914 (dark solid regression line for U(a) dives: dive duration (min)=9.83+1.20 dive depth(m), $F_{1,34}$=16.43, r^2=0.33, $p<0.001$; light solid line for U(b) dives: dive duration (min)=0.64dive depth(m)-1.86, $F_{1,15}$=14.42, r^2=0.49, $p<0.005$.)

5.3.3: Post-dive surfacing intervals:

There is a clear significant relationship between the duration of individual dives and both the post-dive and pre-dive surface intervals for 4394a; this is not as clear with the other turtles and only significant for 21914 (figure 5.38, p. 189). The post-dive surface intervals show a significant relationship with the duration of U-dives performed by 21914 at the foraging ground (figure 5.39, p. 190). There is a similarity with resting dives at Ascension Island from a previous study using TDR data (Hays et al., 2000a). There is no significant relationship between the pre-dive surfacing interval and the duration of the subsequent dive.

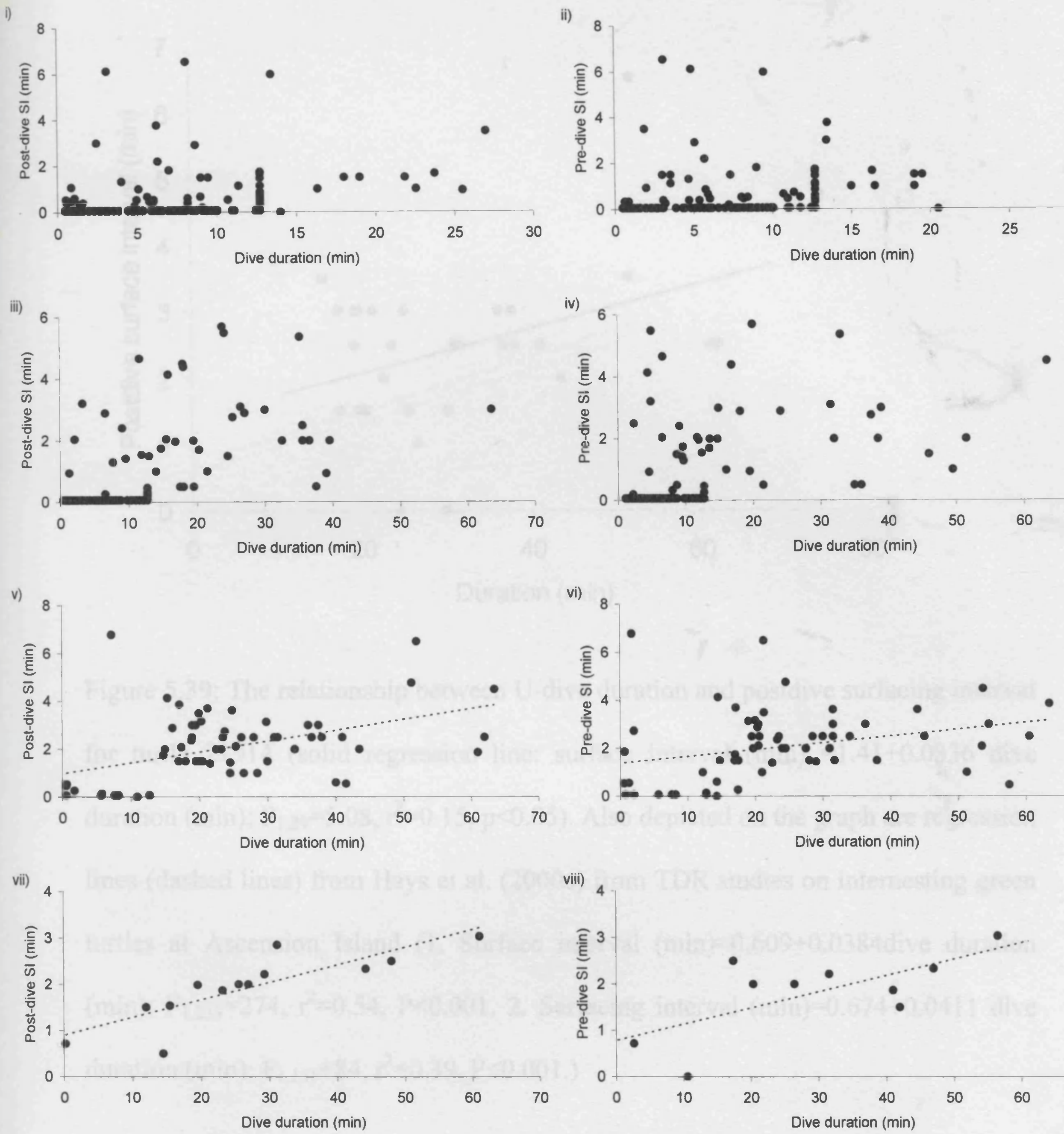


Figure 5.38: Pre- and post-dive surface intervals for all individual dives recorded at the foraging areas for turtles 15119 (i and ii), 15122 (iii and iv), 21914 (v and vi) and 4394A (vii and viii). Regression analysis; i, ii, iii and iv: no significant relationship; v) post-dive SI (min)=1.04+0.0435 duration (min), $F_{1,61}=13.47$, $r^2=0.18$, $p=0.001$; vi) pre-dive SI (min)=1.45+0.0269duration (min), $F_{1,61}=5.31$, $r^2=0.08$, $p<0.05$; vii) post-dive SI (min)=0.905+0.0378 duration (min), $F_{1,11}=26.93$, $r^2=0.71$, $p<0.001$; viii) pre-dive SI (min)=0.785+0.0349 duration (min), $F_{1,8}=6.8$, $r^2=0.46$, $p<0.05$.

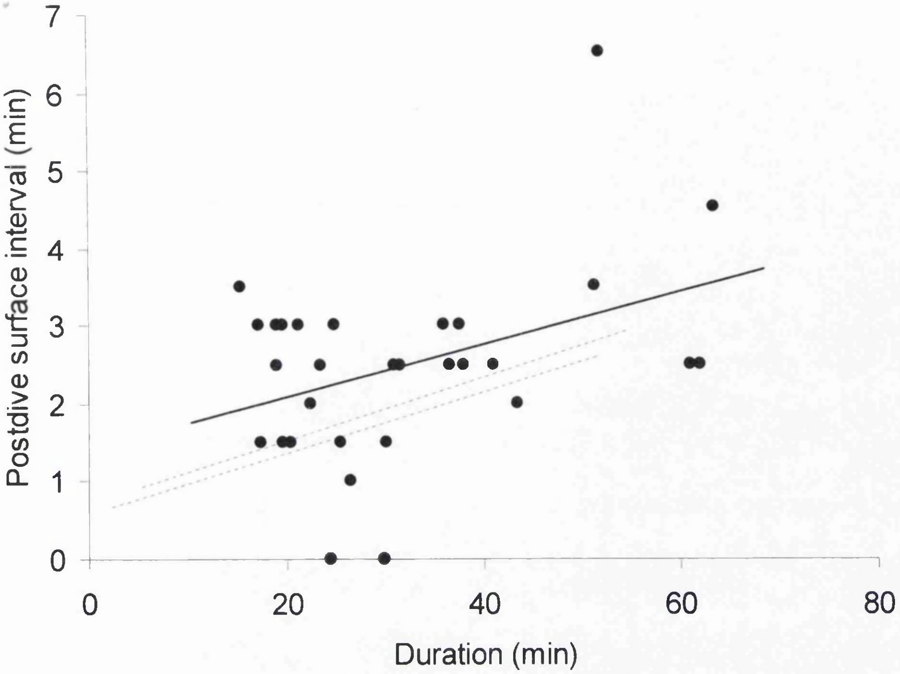


Figure 5.39: The relationship between U-dive duration and postdive surfacing interval for turtle 21914 (solid regression line: surface interval (min) =1.41+0.0336 dive duration (min); $F_{1,29}$=5.08, r^2=0.15, p<0.05). Also depicted on the graph are regression lines (dashed lines) from Hays et al. (2000a) from TDR studies on internesting green turtles at Ascension Island (1. Surface interval (min)=0.609+0.0384dive duration (min); $F_{1,233}$=274, r^2=0.54, P<0.001. 2. Surfacing interval (min)=0.674+0.0411 dive duration (min); $F_{1,131}$=84, r^2=0.39, P<0.001.)

CHAPTER 6

Discussion

6. Discussion:

The movements and behaviour of marine turtles have broad and important ecological implications (Troëng et al., 2005). They fill important ecological roles through energy transport, nutrient cycling and by affecting community structure (Bjorndal, 1997) (e.g. introducing nutrients into beach ecosystems which helps maintain stable dune systems (Bouchard and Bjorndal, 2000)). A poor understanding of the distribution and movement of many marine vertebrates has impeded conservation of these species (Block et al., 2001). Identifying the location and size of marine turtle habitats for both migrations and foraging are needed in order to determine their ecosystem roles and identification of priority areas for protection is necessary to ensure marine turtles fulfil their ecological roles (Troëng et al., 2005). Anthropogenic threats may vary greatly between habitats during the life history of a turtle; longline fisheries may threaten turtles during oceanic migrations whereas directed take and incidental capture by smaller fisheries are critical in the neritic foraging zone (Lutcavage et al., 1997). Globally, the green turtle is classified as endangered and the population is estimated to have declined by 48 to 67% over the last 3 generations (Seminoff, 2004). Even at Ascension Island where the nesting grounds are afforded a high level of protection and localised foraging areas of this population off Brazil have been designated protected areas, the population appears to be a fraction of that which existed centuries ago (Broderick et al., 2006).

Long distance migration of green turtles between nesting areas and feeding grounds was first recorded around 1960 (Carr, 1965). Since then, migrations have been charted for many species including loggerhead (*Caretta caretta*) (e.g. Papi et al., 1997) and green turtles (*Chelonia mydas*) (e.g. Papi et al., 1995), with migration routes covering distances of up to 4000km (Mortimer and Carr, 1987). Originally tags were simply attached to the animal and collected at nesting grounds (mark-recapture studies) and then satellite transmitters allowed the routes to be identified. New technology allows dive data to be collected as the turtle travels and is leading to a greater understanding of the animal's behaviour at sea. Up to now green turtles migrating away from nesting areas have only been studied with transmitters that provide summaries of information or limited dive parameter data. Diving data can now be closely analysed in terms of the different dive types and their relationships to other parameters e.g. time of day and dive duration, in order to further explain the diving behaviour of these animals in relation to their environment (Putz and Cheryl, 2005). In this study dive profiles were obtained for the first time allowing detailed dive behaviour to be seen. The data set presented an unusual opportunity to study four different phases of the green turtles' life history; internesting, open-ocean migration, coastal migration and restricted area foraging, using the same individuals and technology.

6.1. Location data and migration speed:

When the turtles were followed throughout the whole post-nesting migration until foraging grounds were reached, a clear biphasal migration was seen for all but one individual with an oceanic and a coastal stage of migration. The turtles tracked across the South Atlantic all reached the coast of Brazil in different places and then travelled varying distances, until ceasing long-range movements in clearly defined habitats. It was interesting to note that some turtles passed through the foraging areas chosen by other individuals and continued migration. Also, a couple of turtles selected foraging areas within a few kilometres of each other but always maintained distinct and separate home ranges. Individual 21914 passed close to Fernando de Noronha on the journey back to Brazil. The fertile, algal rich waters around this island are home to foraging green turtles (Marcovaldi et al., 1998), but there was no evidence that this individual paused migration here. Other tracking studies have shown foraging site fidelity but variation in the migratory path. A green turtle followed on its post-nesting migration from the Cayman Islands conducted a direct oceanic crossing on one occasion and then an indirect oceanic crossing followed by coastal migration on the other to return to the same foraging site (Blumenthal et al., 2006). Tag returns in Australia have also implied similar site fidelity for adult female turtles (Limpus et al., 1992; Limpus and Limpus, 2001).

At the approximate latitude of the study in the Mediterranean, 30°N, an average of 12 satellite overpasses occurred each day (by 2 satellites only at the time of this study) whilst at the equator there were only 6 to 7 (Argos, 1996). This was reflected in the significantly higher quantity of fixes received per day from the Mediterranean turtles during the post-nesting migration. A lower number of location fixes are received per day for turtles 4149 and 4150 during the coastal leg of the migration implying that these turtles appear to be submerged when the satellite passes overhead more during coastal travel than open sea migration. The fixes of these two turtles are also less accurate when travelling in the shallow water than when at sea. This implies less uplinks to the satellite during an overpass, therefore the turtle is submerged for longer periods and at the surface for shorter periods of time. This is consistent with the findings of Byles and Dodd (1989) and Plotkin (1998), implying that the turtles are engaged in shorter and shallower dives during open sea migration and longer dives once at the coast. Plotkin (1998) found a distinct difference between the number and accuracy of fixes whilst satellite tracking 21 olive ridley turtles (*Lepidochelys olivacea*) during internesting and into open ocean. Whilst the turtles were in coastal waters, the number of transmissions was low and the accuracy of the fixes was poor. After nesting, all the turtles moved into deep oceanic waters, where the number of transmissions increased and the accuracy improved. During internesting gravid turtles tend to be inactive and remain submerged for a high proportion of the time. During travelling in open water turtles will spend more time near the surface and hence this leads to more uplinks. If these surface intervals are then longer the satellite will receive more uplinks during a pass and hence the accuracy will be better for the location calculations. Byles and Dodd (1989) noted a similar change in dive behaviour of a loggerhead tracked from coastal to oceanic waters. The submergence behaviour in deep water was significantly different than coastal behaviour. The number of dives increased in deep water and the mean dive duration was less than half of that seen in coastal waters. The Atlantic turtles showed a similar pattern, with significantly fewer locations received from shallow waters during internesting and once off the coast of Brazil compared to open sea migration. There was no significant difference between the number of fixes received per day from Ascension or the foraging grounds implying high submergence times in both.

A significant difference can still be seen between the different legs of the journey for both populations, even if calculating the distance and speed between points over a certain distance or time apart may lead to an underestimation of the true travelling speed (Hull et al., 1997). It is clear that there is a difference between open sea and coastal migration and the turtles slow down significantly when they reach the coast.

There appears to be no correlation between turtle size and the mean speed of travel for the Ascension Island turtles as would be predicted, perhaps as the speed for each individual does not remain constant throughout the oceanic phase. When the noise created by location inaccuracy was filtered out to provide a clearer picture of any changes in travelling speed, it was interesting to note that the speed of only one turtle decreased over time as may have been predicted. One individual's speed fluctuated up and down during the entire migration whilst the others went up and down for the first half of migration and then one remained at a constant speed, one decreased travelling speed and one increased it during the second half. All, however, showed a clear decrease in travelling speed once reaching the Brazilian coast. Individual 21914 is seen to be different from the others travelling faster for greater periods of time. It is the smallest turtle, but the fastest swimmer. The behaviour of this turtle is also distinct as it appears to break up the route back to Brazil with periods of resting or foraging U dives. This is different from the other turtles in this study which show a consistent behaviour pattern of shallow near-surface travel during the day and deeper diving at night. It appears to employ a different strategy than the other turtles showing a more varied pattern of diving with a lower percentage of mid-water dives, perhaps leading to the greater travelling speeds.

When the coastal migration of the Ascension turtles was examined in more detail, a high number of fixes was reported as being inland. By using the depth of dives that were assumed to be to the seafloor to adjust the longitude value of locations, the route became straighter and it became apparent that all turtles prefer to migrate close to the shore at a preferred depth range. This unfortunately makes them more susceptible to anthropogenic threats including fishing and pollution as they conduct the coastal phase of post-nesting migration. In Nicaraguan waters more than 10000 green turtles are caught by fishers each year (Lagueux, 1998). It will be very interesting in the future to see if turtles conduct a coastal phase of migration on the return journey to Brazil, or simply begin directed movements eastward from the foraging areas.

6.2. Diving behaviour:

The amount of diving data varied considerably between the individuals. A lot of dives were recorded with depth values less than 6 m, especially when turtles entered shallow habitats. When studying internesting behaviour, this does not present a great problem. The turtles are conducting dives of a uniform depth and duration and as in general only the last depth value was a zero, correcting the dive is easy as this final portion of the dive represents only a small percentage of the dive duration. During foraging, some turtles were in very shallow habitats and dives profiles were received that had more than one zero value. In these cases it is not as easy to assume that the zero value is simply a missed end point as it could quite easily be an inflection point in the top 6 m of the water column.

The highest proportions of dives recorded during the study were U dives and type 3 midwater dives. This is as would be predicted from the results of TDR studies on internesting and displaced turtles (e.g. Hays et al., 2001a). The U dives were also distinguishable into two types depending on the bottom time and depth/ duration ratio (as in Houghton et al., 2002). This ratio can be used as an indication of activity levels. Dive depth and duration have a close relationship as the deeper the turtle dives, the more air it can store in the lungs and not have to fight to overcome buoyancy

(Minamikawa et al., 1997). As activity levels increase this oxygen will then be used up quicker and dives will be shorter. For all different turtle dive types, maximum depth and duration are seen to show a significant correlation although there are substantial differences between dive types in best-fit curves for this relationship (Hochschied et al., 1999).

Although the amount of data received showed a big variation, overall behaviour patterns were very similar between the individuals. For turtles that provided an internesting record, dive behaviour was dominated by U dives of a preferred depth. These are known to be for resting purposes as there are no foraging opportunities for turtles around Ascension. The median depth of these U dives did not appear to show a relationship with the turtle CCL measurements though this study was only a small sample size.

As the turtles begin the first phase of migration away from Ascension Island, a transformation in behaviour occurs associated with cost efficient migration strategies. As foraging is not possible during the whole time away from the Brazilian coast, all the behaviour seen will be governed by the need to conserve as much energy as possible. Cost of Transport (CoT) is of critical importance in an animal's life-history (Miller et al., 2004). It influences migration speed, foraging and social behaviour (Sumich, 1983; Connor et al., 1998), and natural selection should favour adaptations that reduce these costs (Vogel, 1981). As well as adaptations like a streamlined body to reduce hydrodynamic drag (Williams, 1999) and fins to generate lift (e.g. Fish, 1996), behavioural flexibility is of importance to reduce energy expenditure whenever possible (Fedak and Thompson, 1993). During the oceanic crossing there was a bimodal distribution of dive depths with a high proportion of shallow dives in the top few metres of the water column and a second peak of deeper dives between 10 and 20 m. This supports previous studies that have seen a dichotomy of dive behaviour where turtles engage in shallow travelling dives near the surface and deeper midwater dives (e.g. Hays et al., 2001a). The dive profiles were dominated by type 3 dives which were mostly recorded at night. Each turtle seemed to have a preferred depth for these dives though this was not related to turtle size. The turtles therefore appear to engage in active surface swimming during the daytime. These surface travelling dives have been identified before and are the most cost efficient way of swimming. By diving down to a few metres below the surface, the turtle avoids the effects of surface drag (Hertel, 1966) but does not spend time and energy swimming down deeper than necessary. The type 3 dives that are mainly seen at night were originally proposed as resting dives (Hays et al., 2001a). The profile shape shows a steady ascent phase after the initial descent and it was thought that the gradual decrease in depth during the dive was an effect on the depth of neutral buoyancy as oxygen stores were used up. Since then activity sensors have show that this bottom phase involves swimming (Hochscheid et al., 1999). The swim speed sensors deployed in this study show that the bottom phase involves as much activity as the descent phase with similar values for swim speed seen through the dive cycle. The overall speed has been seen to be lower for migrating turtles during the night compared to day (Luschi et al., 1996; 1998), but this is therefore due to the time spent diving down to depth rather than a lack of activity or resting behaviour. The exact purpose of these midwater dives is not fully understood. It has been proposed that they are for predator avoidance as diving below the surface, the turtle will reduce the extent to which they are silhouetted against the surface (Hays et al., 2001a). The surface appears to be the most dangerous place in the water column for air-breathing animals that are attacked by sharks and green turtles may dive in a way that minimises the risk close to the surface (Heithaus et al., 2005). Satellite tracking in Japan has suggested that green turtles may not necessarily be obligate herbivores that need to return to neritic habitats to feed (Japan Fisheries Resource Conservation Association, 1999) and one post-nesting turtle conducted oceanic wandering for 8 months of tracking. It was proposed that deeper night time dives enabled turtles to forage on macroplankton that exhibit diel vertical migration (Hatase et al., 2006). Leatherback turtles feed on the deep scattering layer at night, reflected in short, shallow and more frequent dives than daytime (Eckert et al., 1989) though these foraging dives tended to be deeper than 30 m, much deeper than the depths of the midwater dives recorded here.

As the turtles approach shallow water after oceanic migration they are seen to conduct deep S shaped dives which are similar to type 3 dives but include an initial deep descent before the gradual ascent phase. The purpose of these dives has been proposed as the turtle exploring the water column as it approaches shallow habitats (Graham et al., 1975; Martin, 2003). Deep dives greater than 50 m in depth were seen for 3 individuals as they got close to Brazil, though a range of shapes were seen for these dives. A similar pattern was seen in all cases with behaviour dominated by midwater dives before the deep dives and then U dives after. Even during bouts of deep dives, the surfacing time in between was short implying they were aerobic. Green turtles have been seen to conduct very deep diving behaviour and hence dives of this depth and duration are probably well within their aerobic capacity (Houghton, 2001). Deep dives have been recorded up to depths of over 50 m in internesting turtles and post-dive surface intervals were not extended indicating these dives were within the physiological capabilities of the individual. When relating the depth and duration relationships of these deep dives to other dive types, the duration is relatively short, implying a higher activity level, perhaps associated with the effort of achieving such depths.

For each turtle, all the dive profiles show a narrow depth range as they migrate along the coastline, implying they are diving close to the seafloor during all types of dives, and as the U dives tend to be to a constant depth, this indicates the turtles travel along the coastline at a preferred depth or distance offshore. The dive record for 21914 is sufficient enough to examine the dive types in more detail during this migration phase. The behaviour is dominated by U dives though these tend to be much shorter than those seen at Ascension. The time spent within 2 m of the maximum dive depth is a good gauge for activity levels of the dives. It was very varied for the coastal U dives compared to those seen during internesting (mean ± SD; coast 67.9±28.6, Ascension 91.66±3.52; t-test, T85=-7.63, p<0.0001). This implies that the diving behaviour during the coastal section of post-nesting migration includes a proportion of active dives to the sea floor supporting suggestions that this phase provides an opportunity to 'refuel' on the return journey (Godley et al., 2002).

6.3. Speed of travel and diving behaviour:

The type of transmitter used in the Mediterranean study recorded dive depth and duration in 6-hour histogram bins so no information is available on individual dives. Even so, these transmitters recorded enough information that a comparison could be made between the diving behaviour and speed of travel allowing deductions on the travelling behaviour of the turtles as they migrated.

During migration there is a clear dichotomy of dive behaviour during the open sea leg and during coastal migration. There is a clear linear relationship between the mean dive depth and duration, with shorter and shallower submergences at sea and then longer deeper dives once the turtles reached the coastal waters. Looking at mean submergences over 6h periods can give a general idea of patterns of behaviour but it is quite possible that the impact of a few long submergences during a 6 h interval may be missed if there are also a high number of short dives (Hays et al., 2001a).

There is a clear diel pattern of diving behaviour during the open sea phase of migration. During the night (period 0) dives were generally deeper and longer, there was a lower proportion of time spent on short and shallow dives and the speed of travel was significantly lower than during the other periods of the day. Long dives greater than 20 min in duration were only seen at night. This is consistent with other studies of migratory diving behaviour in green turtles that have also found significant differences between day and night dive depths and duration (Papi et al., 1997; Hays et 2001a). Green turtles migrating from Ascension Island to Brazil have been seen to engage in some longer submergences at night, over 20 min in duration (Hays et al., 2001a), though most submergences were less than 5 min long at a depth of around 1 m, consistent with predictions for optimisation of near-surface travelling. Internesting turtles at Ascension Island also showed a diel pattern to their diving behaviour (Hays, 2000a). A greater proportion of time at night was spent on resting dives over 20min in duration than during the day.

When comparing the speed of travel with dive data from corresponding 6-hour periods, comparisons can be drawn on where the turtle swims in the water column, the duration of submergences, and how this determines the speed of travel. 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, 1993). Oxygen consumption generally increases with swimming speed. The amount of oxygen that an animal stores and how rapidly this is used up during diving both influence how long a diving animal can remain submerged (Hindell et al., 2000). As speed increases, the scatter of the mean depth of dives in that 6h period becomes less. At slow speeds the turtle can dive to a range of maximum dive depths as oxygen use will not be such an important issue determining the duration of the dive and hence depth achievable. As speed increases then oxygen use becomes a factor in determining the duration and hence depth of a dive and the turtle can only engage in shallow dives. Dive duration and depth are related and high levels of activity will mean that the turtle cannot remain submerged for long periods of time and still utilise aerobic respiration. Dive duration relates to activity during a dive, slower swimming or resting leads to a reduced rate of oxygen consumption and longer dives (Hochscheid et al., 1999). It therefore follows that the mean submergence duration will decrease with increasing speed as the time spent on short travelling dives increases. This relationship has also been seen in Northern elephant seals which exhibit a strong negative relationship between dive duration and speed suggesting that the faster the animal swims the quicker oxygen stores are used up (Le Boeuf et al., 1992).

In this study, it is seen that the proportion of time spent engaged on short and shallow dives increases linearly with speed. When travelling, to maximise efficiency of energy intake, speeds should be close the minimum cost of transport (Thompson, 1993). The energetic demands of long-distance migration are high, therefore turtles must maximise their energy expenditure as they cannot feed en route (Southwood et al., 1999) and therefore they travel at the most efficient speed. Migrating turtles tend to show a high proportion of dives that are short and shallow (Balaz, 1994; Hays et al., 2001a). It is not advantageous, therefore, to swim too far down in the water column as time and energy is wasted when surfacing to breathe and then diving down deep again. Marine air-breathing animals that swim on the surface are limited in their performance by the large amount of energy dissipated in the production of a wake, and hence have been shown to have rather high costs of transport and low efficiencies compared to animals swimming deeply submerged (Prange, 1976). The least drag and hence lowest costs are seen to be when an animal swims at a depth of at least 3 times its body diameter. Therefore they must use the most efficient swimming behaviour and swim as shallow as possible but not directly at the surface. Therefore the swimming behaviour of the turtles in this study is as would be predicted, travelling at the most cost efficient way engaging in short travelling dives of a few minutes just far enough below the surface to avoid significant drag effects.

When comparing the speed of travel with the diving behaviour of the Mediterranean turtles, there is a variation between the individual turtles. Different factors appear to influence the speed of travel for each turtle. There may be more variation in the dive behaviour of turtles 4149 and 4150 as they are undertaking relatively long migrations compared to turtle 4148 that only has a short migration of around 2 days until she reaches shallow coastal waters. No dives over 20 min were seen during the open sea migration of turtle 4148. When the speed of travel of turtle 4148 is compared to the diving behaviour, it is seen to be very closely related to the proportion of dives that are less than 5 min in length. Again this would be consistent with optimising energy use. There is more variation in the effect of different variables on the speed of travel for turtles 4149 and 4150 that migrate south to the coast of Africa. Turtle 4150 shows a positive relationship between speed of travel and shallow dives. The variation in behaviour of the latter two turtles could be due to the longer migration that has a significant portion of coastal travel. The turtles could therefore be choosing a wide range of different behaviours as well as cost efficient swimming in order to conserve energy. These could include more resting or foraging once they reach the coast.

Thus dive behaviour can be seen to have a direct effect on the overall speed of travel simply due to the fact that an increase in depth corresponds to greater dive angles leading to a decreased horizontal component per unit time, which effectively decreases horizontal speed. There is a clear delineation of speed between open sea and coastal migration, corresponding with a change in diving behaviour. Also, there is a clear difference between day and night behaviour during open sea migration with a nocturnal increase in dive depth and duration and a decrease in speed of travel. As the dive behaviour of the turtles in the Mediterranean Sea is recorded in 6 h histogram bins, a record is not produced of the depth and duration of individual dives. So in a 6-hour period, the turtle may be engaged in both shallow and deeper dives. During coastal migration, a 6 h interval may include foraging, resting or travelling behaviour for different proportions of the time. Even so it can be seen there is a clear relationship between speed of travel and diving behaviour. Short and shallow dives lead to a faster travelling speed and this is seen to be the typical behaviour during the open sea phase of migration. Coastal migration leads to a reduction in the travelling speed. It can be assumed that if there is foraging available once the turtles reach shallow water then travelling in the most cost efficient way may becomes less of a necessity.

The Ascension Island turtles performed a much greater oceanic migration than those in the Mediterranean Sea. They also showed a dichotomy of migratory behaviour reducing travelling speed dramatically in shallow coastal waters compared to oceanic waters. Studies comparing speed of travel in migrating turtles have found distinct differences between open sea and coastal migration (e.g. Cheng, 2000). Unlike the Mediterranean data set, the fixes were not received in sufficient quantity to allow comparison of dive behaviour and speed of travel in 6 hour periods. Even so, it appeared that speed of travel correlated with the average dive depth and percentage of time deep; speed decreasing as more time was spent on deeper diving, i.e. less time spent on near-surface travelling dives which have been shown to be the fastest way to travel. The actual depth of the shallow dives also showed a relationship with the overall speed of travel. As the modal depth increased, the speed decreased. There appeared to be a correlation between the depth of the midwater dives and the speed of travel; the deeper the dives, the slower the travelling speed. A clear significant relationship between speed of travel and diving behaviour was not seen with these turtles as it was with the Mediterranean turtles. This may be due to the paucity of data leading to comparisons being made in 2 day means. Also with fixes being of the lower accuracy classes, the distance between consecutive fixes used for speed calculations means that the speed may be underestimated. The speed of travel was found to be related closely to the distance and time between the two fixes used for the calculation and greater separation may lead to more severe underestimates of rates of travel (as seen in Hull et al., 1997).

As the oceanic migrations progressed, the number of shallow dives was seen to drop for all turtles and the percentage of time spent engaged on deeper dives increased. The reason for this is not fully understood. Perhaps the midwater dives expend less energy than near-surface swimming and the turtles would tire and want to conserve more energy as migration progressed.

There was a relationship between the size of the turtles and the midwater diving behaviour (although the sample size is small). The two larger turtles appeared to spend more time conducting these dives than the smaller ones and they were longer in duration too. Allometric studies have previously demonstrated positive trends between body size and dive duration across many taxa of air-breathing divers (Halsey, 2002). Larger diving animals have a body mass advantage, as body mass increases more oxygen can be stored and metabolised more slowly in relation to their body size. When body mass is related to dive duration, larger species dive for longer to a given depth. Larger animals that dive shallowly, probably for ecological reasons such as water depth, make use of the physiological advantage that their size confers by diving for longer (Halsey et al., 2006).

6.4. Home range and foraging areas:

It is important to study the foraging areas of the turtles tracked from Ascension Island as the majority of studies on this population so far have been during internesting. Location filtering was used to try and define the size and depth of areas used by the turtles and it was seen how important it is to accurately filter locations as it can alter the perception of the area. For example, for 4394A, the mean position moves 20km further offshore into deeper water after filtering. There were some very inaccurate fixes provided by the transmitters during the foraging phase. In the most extreme case a LC B fix was reported to be 235km inland! Overall, the filtering process provided a good indication of the home ranges of the turtles and allowed foraging areas to be compared. As in Godley et al. (2003), when allowing for the inaccuracies of satellite derived locations, turtles were seen to maintain distinct home ranges centred around different depth ranges. The standard deviation of the distance of fixes from the mean position was often less than those predicted by Argos implying restricted movements for all turtles. Turtle 15119 had a higher calculated standard deviation for longitudinal movement compared to latitude corresponding with its habitat along an east-west coastline, whereas 21914 showed more latitudinal variation corresponding to its position along the north-south coastline.

There was no correlation between turtle size and the depth selection seen as would be predicted, though a larger data set would need to be examined to verify this. In fact, the smallest turtle resided in the deepest habitat. Little research has been conducted on the home range of marine turtles and substantially different home ranges sizes of marine turtles have been reported (Yasuda and Arai, 2005). The method used to establish the home range may influence the results. When using sonic or radio telemetry to track turtle movements, the results could be biased by many factors including field conditions and degree of effort, whilst satellite tracking may overestimate home range sizes because of location inaccuracies. Varying results have also been seen when comparing turtle size to habitat use; Mendonca (1983) reported juvenile green turtle size affects the home range size, whilst Seminoff et al. (2002) reported no such significant size effect on home range area.

It was seen that turtles in deeper water had a larger home range than those in shallower water. After filtering, more scatter was seen in the fixes from turtles in deeper water compared to those closer to shore. This reflects the pattern seen with increasing latitude on terrestrial species. As increasing latitude is broadly associated with decreasing productivity it would be expected that the size of the home range of a given species will increase with latitude (Harestad and Bunnell, 1979). Animals having difficulty meeting their energetic requirements in a low-productivity habitat would need to make more extensive movements (nutritional search) and therefore, have larger home ranges (Kaufman, 1995). This latitudinal effect has been recorded in wood turtles (*Clemmys scripta*) where home ranges were larger in more northern populations than southerly ones (Arvisais et al., 2002). Therefore it can be hypothesized that the increase in movements that corresponds with increasing depth for the turtles residing off the coast of Brazil may be a function of productivity as food availability will decline with depth as light levels fall.

6.4.1. Behaviour at the foraging areas:

For the first few months at the foraging grounds all three Mediterranean turtles showed a significant diurnal difference in mean dive duration, with a higher proportion of longer dives during the night than during the day. This is characteristic of green turtle foraging behaviour, though green turtles have been observed to feed at night (Bjorndal, 1980; Ogden et al., 1983; Balaz et al., 1987). When Seminoff et al. (2002) tracked green turtles in the Gulf of Mexico using radio and sonic telemetry, diurnal sightings were in deeper depths than at night. This behaviour was seen to be influenced by avoidance of human disturbance in the shallow water during the day. Submergence intervals when herbivorous turtles feed are generally less than 10 min and more than this when the turtle is resting, on average 20 min (e.g. Brill et al., 1995; Davis et al., 1999; Rice et al., 2000). In this study, by considering the time spent engaged on dives less than 10 min in duration and in the surface 2 m, this should identify foraging behaviour.

In the present study, two of the turtles (4149 and 4150) showed a diel pattern in the mean dive duration but not dive depth. It has been inferred that turtles rest in deeper water than where they forage as they can attain neutral buoyancy with a larger lung volume at deeper depths, and therefore remain submerged for longer periods of time (Minamikawa et al., 2000). Turtles 4149 and 4150 were resident in enclosed shallow bays of a maximum depth of 5m and would not have deeper resting sites available close to their foraging areas. Therefore dive depth did not show variation for these two turtles and mean dive duration was shorter throughout the 24h cycle implying shorter resting dives due to shallower depth. Turtle 4148 showed a marked variation in the maximum dive depth during each 6h period when compared to turtles 4149 and

4150. This can be compared to the bathymetry of the foraging areas (see Godley et al., 2002 for maps). The turtles off the coast of Libya resided in, or close to, shallow bays before winter that have a maximum depth of 5m, and then moved offshore into deeper water up to 20m deep. This implies that the turtles were diving to the seafloor as their maximum depths corresponded so closely to the bathymetry in each location. The area in which turtle 4148 was resident is a coastal area with much steeper bathymetry offshore, and therefore small changes in location could lead to a change in seafloor depth. This would agree with the turtles diving to the seafloor and hence in shallow areas depth of dives will not be so dependant on behaviour, whether feeding or resting, but the location of the turtle.

At the foraging grounds off the Brazilian coast two different behaviour patterns were recorded with two turtles selecting shallow habitats and two in deeper water. The shallow turtles showed diel patterns of behaviour as seen with the Mediterranean turtles; short and shallow diving during the day and deeper, longer dives at night. The dive profiles that were recorded showed no depth difference but were longer in duration at night. For both turtles in shallow water, shallow dives dominated the daytime diving record. These are recorded with less precedence than the profiles and hence the high number of these dives implies little diving over 6m during the daytime.

Turtle 21914 resided in much deeper water off the coast of Brazil than the other turtles. The majority of profiles recorded were U dives. The duration of these was shorter in the daytime but no significant day/night difference was seen in the depths. The dive profiles recorded during the daytime for turtle 21914 were mostly U(b) dives, whilst U(a) dives dominated at nighttime. Therefore it can be concluded that this turtle was engaged in active U shaped dives during the day time for foraging or exploratory purposes and then diving to the seafloor at night to rest. There appeared to be peaks of activity mid morning, mid afternoon and at dusk. This corresponds with visual observations made on juvenile green turtles by Ogden et al. (1983). They were seen to be inactive during the night and at midday and engaged in two feeding bouts, one in the morning and one in the afternoon (Ogden et al., 1983). TDR studies on green turtle foraging have also shown peaks of activity mid morning and mid afternoon. Green turtles in a creek in the Bahamas were observed to move out of sleeping areas shortly after dawn and then feed intermittently throughout the day but with 2 peaks of activity around mid morning and mid afternoon (Bjorndal, 1980). Little activity was observed during the night, except for occasional surfacing for breathing and occasional feeding on bright moonlit nights. Hawksbills (*Eretmochelys imbricata*) (van Dam and Diez, 1996) which are spongivorous, have also been seen to exhibit diel patterns in their foraging behaviour, foraging during daylight and returning to resting areas at night. This is opposed to data on loggerheads and Kemp's Ridleys (*Lepidochelys kempii*), which are omnivorous, feeding on prey that is mobile, widely dispersed and nocturnally active (Schmid et al., 2002). Leatherbacks also feed at night with dive patterns correlated to the diel migration of zooplankton (Ekhert et al., 1989). Although, more recently, studies have shown that leatherback turtles vary diel behavioural patterns between foraging and migratory behaviours associated with changing resource conditions (James et al., 2006b) and also they can switch nocturnal and diurnal activity during migration as local conditions change (Hays et al., 2006).

When comparing the U dives of 21914 at the foraging ground to those seen at Ascension during internesting (Hays et al., 2001a), it is interesting to note that even the resting dives at the foraging ground are well below the regression lines drawn for resting internesting turtles. Perhaps the metabolism is slowed in these turtles at Ascension. Without the opportunities to forage around Ascension, energy conservation is incredibly important and even the more active dives during internesting are longer for a given depth than those recorded off the Brazilian coast.

6.4.2. Post-dive surface intervals:

There is no significant relationship seen between the duration and depth of dives and the corresponding post-dive or pre-dive surface intervals for the turtles that resided in shallow water habitats unlike those in deeper water. Predictions from what is known about energetics and turtle diving behaviour would suggest that the time the turtle spends at the surface replenishing oxygen stores would be linked to the time the turtle spends underwater (Hays et al., 2000a). As resting turtles are known to regulate their buoyancy through lung volume, this surfacing period could also be predicted to be linked to the depth at which the turtle is diving and the size of the oxygen store of the turtle. For each individual turtle, a relationship should be seen between the diving behaviour and the pre-dive surface interval as the turtle selects the volume of oxygen to take to the required depth. If the turtle is engaged in aerobic behaviour which would be the prediction for cost-efficient behaviour, then there would not necessarily be such a strong relationship between the surface time after a dive and the duration and depth of the dive beforehand. The results seen here imply that deeper turtles prepare for the depth of the dive and inhale a corresponding volume of air before submerging, whereas shallow diving turtles can only take in a relatively small volume of air before each dive or they will spend a great deal of energy overcoming positive buoyancy to remain underwater. As the surface intervals can only be calculated when bouts of diving are recorded, the pre- and post-dive surface intervals tend to show a very similar distribution when compared to dive depth. All the surface intervals were short implying aerobic diving. Even when turtles engaged on dives deeper than 50m, the surface intervals were short. The relationship between the PDSI of 21914 at the foraging ground showed a close similarity to that reported for turtles at Ascension Island from TDR studies with an increase in surface intervals as dive duration increased (Hays et al., 2001a). This indicates a relationship between dive depth and surface duration controlling for dive duration suggesting that deeper dives are energetically more expensive than shallow dives of the same duration (Halsey et al., 2006.)

6.4.3. Seasonal movements:

The movements offshore and the corresponding change of behaviour occurred when water temperatures dropped from 30 to 25°C for turtle 4148 and 25 to 20°C for turtles 4149 and 4150. This pattern of seasonal movement has been recorded in other populations of turtles. Adult and sub-adult loggerheads and Kemp's Ridleys off the coast of Florida have been seen to move in response to changing water temperature, generally showing directed movement when water temperature dropped to below 15°C (Nelson, 1999; Standora et al., 1990). As water temperature dropped, the turtles moved offshore and south. When the water warmed up again next spring the turtles moved back to the same vicinity they left in the autumn. Loggerheads in the Gulf of Mexico were recorded moving offshore due to a cold front (Renauld and Carpenter, 1994). Most migratory patterns have been recorded in Kemp's Ridleys and loggerheads. Green turtles are generally tropical and subtropical, whilst Kemp's Ridleys and loggerheads spend much time in warm temperate waters, showing seasonal temperature related migrations between high latitude foraging and lower latitude over-wintering grounds (Davenport, 1997). Cold stunning, or extreme hypothermia, is reported to occur in captivity when water temperatures are less than 9°C (Schwartz 1978). In the wild this has been observed when water temperature drops below 8°C before turtles can swim away from an area during the sudden onset of a cold front (Witherington and Erhert, 1989; Morreale et al., 1992). They suffer from a loss of the ability to swim, dive or regulate buoyancy.

Green turtles, being herbivorous, are reliant on shallow coastal habitats where seagrass and algae will be abundant during the warmer months. During the winter it is likely that the productivity of such areas will decrease and hence the movements recorded offshore could be due to avoidance of colder temperatures in shallow water and possibly due to a lack of suitable food. If this is the case, the turtles may have to rest and conserve energy until the spring initiates new growth in the food plants. The long dives seen over winter are probably due to turtles entering a state of quiescence in order to minimise their energy expenditure over winter until they can return inshore and begin to feed again in the spring. The eastern basin of the Mediterranean Sea has been shown to have an average lower productivity than the western basin (Turley, 1999) with a significant lack of food availability during the winter months. Loggerheads off the coast of Tunisia are subjected to similar seasonal changes in temperature as the turtles studied here off the coast of Libya, and although they reduce activity they continue to forage (Laurent and Lescore, 1994) as their pelagic lifestyle during the winter means that they can remain active and find food. Whereas loggerheads in artificial environments that were subject to a seasonal decline in water temperature underwent profound reductions in oxygen consumption in the winter temperatures (Hochschied et al., 2004). Activity was greatly reduced and submergence intervals increased. No circadian rhythm was detected in activity or oxygen consumption. The seasonal change in oxygen consumption was matched by a decrease in food consumption. Water temperature also affects digestive efficiency (Bjorndal 1980) and it has been seen that turtles show greater variation in digestive abilities during the cooler months of the year. Kemp's Ridley turtles generally leave coastal areas prior to the onset of low water temperatures and weight loss has been recorded in individuals that remain too long suggesting they experience a negative effect from the lower water temperatures (Standora et al., 1990).

The changes in dive duration seen in this study agree with findings from other telemetry studies. Loggerheads tracked in the Gulf of Mexico showed seasonal and diel patterns to their submergences (Renauld and Carpenter, 1994). There were significantly longer submergences and fewer dives recorded during the night in all seasons, and the lowest number of submergences were recorded during the winter. Similarly a Kemp's Ridley turtle showing typical seasonal coastal migration was tracked along the Georgia coast (Gitschlag, 1996). The adult showed seasonal and day/night differences in average submergence duration, with longer dives at night during all seasons. This study clearly shows a change from typical foraging behaviour with diel patterns in activity in the autumn, to different wintering behaviour when, as temperatures drop, the time spent on foraging drops rapidly and although there is still a higher number of short dives during the day than during the night, this is considerably less than during the autumn. Activity of green turtles is shown here to be correlated to dive depth and temperature of the surrounding water. When diving deeper, turtles are engaged in less active short foraging dives, and this is also the case as temperature drops. Whether the temperature drop causes the lack of activity due to lowering the metabolic rate, or if the turtle ceases feeding and rests in order to adapt to a lack of foraging opportunity in the winter months is unclear.

At the beginning of spring, two of the turtles moved back into the same shallow water areas where they had been resident in the autumn. The change in behaviour seen at this time corresponded with a lower temperature change than that at which they began over-wintering. A rise from 17 to 22°C corresponded with the increase in activity. In laboratory studies turtles have also been found to become more active at lower temperatures (Moon et al., 1997) and it could be that although the temperature is still lower than optimum, the increase acts a trigger for spring and the turtles become active again. The turtles may become inactive at a higher temperature range in the autumn as this drop may be a signal to adapt their behaviour to conserve energy ready for further temperature drops.

The changes in behavioural patterns over winter are comparable to the findings of studies into temperature change on turtle metabolism and feeding behaviour. Temperature has a profound effect on the oxygen consumption in reptiles and, between 10 and 30°C, oxygen consumption for resting and routinely active turtles increases with temperature with Q_{10} values of between 2 and 3 (Lutz et al., 1989). Reduced temperature has been seen to lead to a lack of feeding, although it is not known if the lack of appetite is due to the cold or an adaptive response to help lower the metabolism and survive the cold. Measurements of metabolic rates in juvenile green turtles (Prange, 1976) show at rest rates up to 4 times lower than while swimming and also by fasting turtles can actually reduce their metabolism by a significant amount. Inactive turtles in laboratory studies that were being subjected to colder temperatures showed no difference in weight compared to turtles being kept in normal 25°C water even though the lowered temperature meant they were fasting (Moon et al., 1997). Wintering freshwater turtles have empty guts and even at warm temperatures, fasting may reduce metabolic rates by 69% (Ultsch, 1989). In the freshwater painted turtle (*Chysemys picta belli*) at 3°C, the combination of fasting, cold and anoxic submergence caused a decrease of metabolic rate of 99% relative to the aerobic rate at 20°C. Sudden drops in temperature cause a lack of feeding and ultimately death, whilst turtles that have been introduced to colder water on a more gradual basis cease feeding and become inactive but tolerate the cold conditions (Hughes, 1974). Painted turtles (*Chrysemys picta*) cease feeding when water becomes too cold in the autumn, and enter deeper water (Sexton, 1959). It is clear though that temperature is a very important cue for entrance into hibernation for turtles (Ultsch, 1989). Hibernation season starts earlier at higher latitudes and turtles disappear earlier at a given latitude when colder weather arrives earlier. Over-wintering behaviour may therefore not only be triggered by temperature but other factors including photoperiod or a reduced food supply. The behaviour of the Mediterranean turtles in this study reflects laboratory studies where feeding in green turtles decreased significantly as the animals were cooled, ceasing at water temperatures lower than 15°C (Moon et al., 1997). They exhibited increased submergence time as the water temperature decreased. Tracking studies have shown temperature affects behaviour in wild turtles with Kemp's Ridley turtles conducting longer submergences as water temperature decreases (Gitschlag, 1996; Schmid et al., 2002). Loggerheads in the Gulf of Mexico tracked by satellite telemetry also showed seasonal differences. One turtle moved offshore in response to a cold front, and the average submergence time was significantly higher during the winter months (Renauld and Carpenter, 1994).

6.5. Conclusion:

With the Mediterranean data set, a high proportion of the locations received for the open sea phase were assigned a high accuracy class and therefore I wanted to see if the speed of travel could be related to diving behaviour. Obtaining the data set in 6 hour bins meant that if a location had been received close the beginning and close to the end of that 6 hours then I had a complete record of the behaviour in that time to compare with speed of travel. For these individuals, a clear relationship was seen between shallow diving and speed of travel. This is in contrast to the open sea phase of the Atlantic crossing, where due to the lack of uplinks from the proximity to the equator and perhaps more deep diving behaviour, there were fewer locations and hence fewer occasions where I had a complete dive record that could be assigned a speed value of such a small resolution. Speed values for the Atlantic crossing were calculated for days rather than hours. Due to the limits of using such transmitters which have proved ideal for obtaining large scale migration information over long periods of time, small scale movements and corresponding diving may not be so easily examined. As technology is developed further, information may become available that would create a clearer picture of the behaviour during the marine wandering of such interesting animals.

Previous satellite tracking studies of post-nesting migration have shown a dichotomy of diving behaviour, long deep and short shallow dives. Short-term TDR displacement experiments have shown long type 3 dives during transit back to nesting areas. This deployment of SRDLs capable of transmitting dive profiles confirmed the similarities of long-distance post-nesting migration compared to short-term displacements with respect to dive shapes and behavioural patterns. It has been shown that dive profiles from SRDLs accurately reflect true dive profiles from TDR data (Myers et al., 2006). Obtaining speed sensor data for these type 3 dives showed conclusively that these dives are not for resting purposes and are indeed travelling dives.

It appears that dive profiles can be used to ascertain behavioural patterns. Activity levels could be assigned to U shaped dives and foraging and resting behaviour could be delineated. For one individual, the results provided by this type of transmitter was detailed enough to delineate active diving during the day and resting at night. All turtles maintained distinct foraging areas upon return to Brazil. A relationship has been seen between water depth and home range size suggesting a link with water depth and food availability. Therefore the SRDLs allowed new insights into post-nesting behaviour and it was interesting to follow the whole return journey back to foraging grounds off the coast of Brazil and have a diving record during each phase.

APPENDIX

AUTUMN	Period	n	Mean	Range	SD	WINTER	Period	n	mean	range	SD	SPRING	Period	n	mean	range	SD
sum (n)	**0**	41	26.5	15-90	12.8	**sum (n)**	**0**	54	6.2	2-20	3.7	**sum (n)**	**0**	18	48.8	12-153	36.4
	1	39	38.0	20-76	12.1		**1**	48	9.3	2-38	6.4		**1**	20	40.6	8-90	21.4
	2	36	16.3	29-67	10.1		**2**	53	16.9	4-76	13.3		**2**	25	29.1	12-79	13.4
	3	30	42.0	28-84	11.5		**3**	53	10.6	3-44	6.6		**3**	24	31.8	13-67	15.9
mean depth (m)	**0**	29	7.9	3.3-11.2	1.8	**mean depth (m)**	**0**	37	12.3	4.8-25.8	5.0	**mean depth (m)**	**0**	14	3.4	2.5-5.8	0.9
	1	31	7.2	3.0-11.3	1.8		**1**	29	12.1	5.5-22.5	4.2		**1**	16	4.2	2.5-7.5	1.3
	2	28	6.4	3.2-8.7	1.3		**2**	33	11.2	5.6-18.5	3.3		**2**	18	6.2	3.7-7.5	1.0
	3	24	6.8	3.9-8.2	1.0		**3**	31	11.0	4-22.5	4.6		**3**	10	5.4	2.5-7.5	1.9
time0-2m (min)	**0**	36	80.1	30-122.5	24.6	**time0-2m (min)**	**0**	30	36.8	0-150	41.4	**time0-2m (min)**	**0**	10	94.8	0-265	88.5
	1	28	69.7	10-127.5	27.0		**1**	33	25.4	0-150	34.2		**1**	12	89.4	47.5-200	52.0
	2	28	51.8	20-137.5	24.1		**2**	37	22.0	0-95	26.4		**2**	15	58.3	10-175	36.6
	3	24	43.8	17.5-70	14.1		**3**	34	33.8	0-127.5	36.5		**3**	22	60.8	30-90	20.3
time 0-10min (min)	**0**	36	34.1	0-295	57.2	**time 0-10min (min)**	**0**	30	4.1	0-37.5	8.3	**time 0-10min (min)**	**0**	10	141.5	45-360	119.7
	1	28	94.0	20-250	55.2		**1**	33	6.3	0-37.5	8.8		**1**	12	78.1	0-187.5	58.8
	2	28	201.7	57.5-322.5	70.0		**2**	37	31.7	0-220	51.2		**2**	15	62.3	0-147.5	45.4
	3	24	184.0	27.5-305	75.4		**3**	34	13.3	0.190	33.1		**3**	22	70.3	2.5-210	58.3
mean duration (min)	**0**	36	12.9	3.6-21.2	3.6	**mean duration (min)**	**0**	30	64.9	22.5-105	24.7	**mean duration (min)**	**0**	10	7.2	2.5-12.3	4.0
	1	28	9.2	3.8-16	2.6		**1**	33	57.3	20.1-105	26.5		**1**	12	11.6	4-38.1	9.0
	2	28	6.9	32.3-10.8	1.7		**2**	37	28.0	3.5-65	13.5		**2**	15	13.0	6-29.6	6.1
	3	24	7.7	4.1-11.3	1.7		**3**	34	40.31	7.3-90	18.7		**3**	22	12.2	4.5-26.4	6.0

Table A5.1: Descriptive statistics of the diving behaviour of individual 4148 divided into 6h periods, 0 (21:00-02:59); 1 (3:00-8:59); 2 (9:00-14:59); 3 (15:00-20:59) local time (GMT+3h). Autumn- 9/8/98-28/9/98, Winter- 11/10/98-8/4/99, Spring- 9/4/99-16/5/99. The dive parameters (and units for the mean, range and standard deviation (SD)) are; the sum (number of dives recorded in a 6 h period) (n), the mean depth of the dives in a 6 h period (m), the time in a 6 h period spent between 0-2 m (not recorded as diving) (min), the time spent on dives less than 10min in duration (min) and the mean duration of all the dives recorded in the 6 h period (min).

AUTUMN	Period	n	mean	range	SD	WINTER	Period	n	mean	range	SD
sum	**0**	33	54.4	14-123	28.0	**sum**	**0**	31	5.6	1-69	12.0
(n)	**1**	33	62.2	20-123	25.8	**(n)**	**1**	24	7.8	1-21	6.1
	2	37	90.6	20-236	52.5		**2**	27	12.2	3-78	14.2
	3	39	100.4	12-221	50.9		**3**	34	7.7	2-32	6.8
mean depth	**0**	25	2.9	2.5-6.8	0.9	**mean depth**	**0**	18	12.1	2.5-25	5.1
(m)	**1**	24	3.6	2.5-7	1.4	**(m)**	**1**	17	10.4	4.2-18.8	4.2
	2	26	2.9	2.5-5.2	0.7		**2**	19	10.4	3.2-15.8	3.3
	3	34	2.8	2.5-12.5	1.7		**3**	25	11.0	3.8-17.5	3.0
time0-2m	**0**	23	32.7	0-85	21.6	**time0-2m**	**0**	24	33.7	0-135	50.7
(min)	**1**	23	25.4	0-62.5	20.7	**(min)**	**1**	16	34.4	0-135	60.1
	2	35	103.7	0-280	92.9		**2**	20	24.6	0-87.5	31.5
	3	27	70.9	0-230	76.8		**3**	22	23.0	0-210	47.4
time 0-10min	**0**	23	146.5	5-350	100.0	**time 0-10min**	**0**	24	0.9	0-10	2.6
(min)	**1**	23	169.6	17.5-305	88.3	**(min)**	**1**	16	9.7	0-47.5	16.3
	2	35	219.9	67.5-360	97.9		**2**	20	20.1	0-257.5	56.5
	3	27	279.4	130-360	80.3		**3**	22	5.9	0-45	12.4
mean duration	**0**	23	8.4	3.8-22.8	5.6	**mean duration**	**0**	24	145.4	49.3-225	80.0
(min)	**1**	23	6.9	3.3-17	3.4	**(min)**	**1**	16	133.9	26.1-225	78.0
	2	35	3.4	2.5-6.4	0.9		**2**	20	55.4	4.4-157.5	38.7
	3	27	3.3	2.6-5.7	0.7		**3**	22	97.4	9.4-225	62.6

Table A5.2: Descriptive statistics of the diving behaviour of individual 4149 divided into 6h periods, 0 (21:00-02:59); 1 (3:00-8:59); 2 (9:00-14:59); 3 (15:00-20:59) local time (GMT+3h). Autumn- 23/8/98-28/10/98, Winter- 29/10/98-26/2/99. The dive parameters (and units for the mean, range and standard deviation (SD)) are; the sum (number of dives recorded in a 6 h period) (n), the mean depth of the dives in a 6 h period (m), the time in a 6 h period spent between 0-2 m (not recorded as diving) (min), the time spent on dives less than 10min in duration (min) and the mean duration of all the dives recorded in the 6 h period (min).

AUTUMN	P	n	mean	range	SD	WINTER1	P	n	mean	range	SD	WINTER2	P	n	mean	range	SD	SPRING	P	n	mean	range	SD
sum (n)	0	45	38.6	11-292	48.1	sum (n)	0	22	2.8	1-5	1.3	sum (n)	0	11	5.4	2-17	4.7	sum (n)	0	28	62.5	8-188	49.2
	1	49	44.1	23-89	11.4		1	18	3.6	1-8	1.5		1	12	15.7	2-47	15.4		1	29	66.6	12-241	48.7
	2	43	74.4	40-152	27.5		2	25	6.0	1-20	5.5		2	17	22.2	9-49	13.2		2	27	73.3	18-162	40.4
	3	49	78.3	36-160	25.0		3	20	4.5	1-20	5.0		3	21	25.4	2-128	30.3		3	34	79.3	12-165	45.4
mean depth (m)	0	37	2.5	2.5-2.5	0.0	mean depth (m)	0	12	15.6	4.5-17.5	4.5	mean depth (m)	0	7	6.8	2.5-12.5	3.5	mean depth (m)	0	23	2.5	2.5-2.5	0.0
	1	39	2.8	2.5-12.3	1.6		1	14	14.9	6.7-17.5	4.3		1	5	6.1	2.7-7.5	2.1		1	22	2.5	2.5-3.1	0.1
	2	32	2.7	2.5-6.7	1.0		2	17	14.2	4.8-22.5	5.3		2	10	5.3	2.5-7.1	1.8		2	22	2.6	2.5-4.3	0.4
	3	34	2.5	2.5-2.5	0.0		3	15	14.9	2.5-22.5	5.3		3	12	5.3	2.5-10.5	3.0		3	27	2.5	2.5-3.1	0.1
time0-2m (min)	0	28	59.5	0-110	30.6	time0-2m (min)	0	16	36.6	0-135	53.0	time0-2m (min)	0	8	17.8	0-127.5	44.6	time0-2m (min)	0	23	101.2	0-320	101.7
	1	41	59.6	0-92.5	21.5		1	10	31.7	0-135	54.5		1	10	3.8	0-20	7.9		1	23	67.8	0-125	44.0
	2	33	70.2	0-195	59.9		2	15	28.7	0-132.5	46.3		2	9	31.1	0-85	32.3		2	19	77.9	0-250	64.9
	3	33	58.3	0-142.5	47.7		3	10	25.0	0-120	42.2		3	12	51.5	0-127.5	46.0		3	21	65.8	0-140	43.2
time 0-10min (min)	0	28	123.0	0-360	106.5	time 0-10min (min)	0	16	0.3	0-5	1.3	time 0-10min (min)	0	8	7.8	0-32.5	12.1	time 0-10min (min)	0	23	176.1	2.5-360	134.6
	1	41	141.0	47.5-285	61.3		1	10	1.2	0-15	4.7		1	10	41.0	0-112.5	39.6		1	23	192.1	25-360	107.0
	2	33	265.2	160-360	66.0		2	15	9.8	0-32.5	10.4		2	9	65.6	10-125	36.3		2	19	214.7	12.5-360	107.7
	3	33	262.3	175-360	59.1		3	10	8.0	0-27.5	11.4		3	12	47.7	0-345	95.5		3	21	217.5	0-360	125.7
mean duration (min)	0	28	11.5	2.9-31.6	6.4	mean duration (min)	0	16	163.8	104.2-225	51.6	mean duration (min)	0	8	131.8	22.6-225	78.6	mean duration (min)	0	23	9.6	2.5-43.8	12.3
	1	41	7.1	3.6-14	2.0		1	10	157.1	74.7-225	59.8		1	10	69.7	9.9-225	74.6		1	23	7.3	2.6-28.1	6.5
	2	33	4.3	2.8-7.5	1.2		2	15	96.0	18.6-225	69.1		2	9	17.0	6.6-41.4	10.7		2	19	5.4	2.5-20	4.5
	3	33	4.1	2.6-6	0.7		3	10	105.6	17.2-225	80.9		3	12	41.1	3-116.2	34.5		3	21	6.8	2.6-22.9	6.6

Table A5.3: Descriptive statistics of the diving behaviour of individual 4150 divided into 6h periods, 0 (21:00-02:59); 1 (3:00-8:59); 2 (9:00-14:59); 3 (15:00-20:59) local time (GMT+3h). Autumn- 21/8/98-28/10/98, Winter Part 1- 29/10/98-8/2/99, Winter Part 2- 9/2/99-31/3/99, Spring 1/4/99-16/5/99. The data are divided into winter part 1 and 2 due to the turtle changing location into shallower water. The dive parameters (and units for the mean, range and standard deviation (SD)) are; the sum (number of dives recorded in a 6 h period) (n), the mean depth of the dives in a 6 h period (m), the time in a 6 h period spent between 0-2 m (not recorded as diving) (min), the time spent on dives less than 10min in duration (min) and the mean duration of all the dives recorded in the 6 h period (min).

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