

# Sea turtles: A review of some key recent discoveries and remaining questions

Graeme C. Hays

*Department of Biological Sciences, Institute of Environmental Sustainability, Swansea University, Singleton Park, Swansea SA2 8PP, UK*

## Abstract

This review highlights some recent important developments in our understanding of the physiological, behavioural and molecular ecology of sea turtles as well as their conservation biology. Key commonalities are identified between the biological questions being addressed with respect to sea turtles compared to those with marine mammals (e.g. pinnipeds and whales), birds (e.g. albatrosses) and fish (e.g. tuna, swordfish and pelagic sharks). Key areas highlighted include (1) objectively identifying oceanic hotspots; (2) measuring what animals are actually doing in different parts of their range (e.g. foraging) rather than simply inferring their state from their position and movement; (3) completing energy budgets for species over ecologically relevant timescales (e.g. the period between breeding seasons); (4) using biological information to help drive conservation management; and (5) assessing the impact of climate change.

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## 1. Introduction

The last two decades have been exciting times for sea turtle biologists. A range of technical developments have provided new tools to capture important aspects of the physiological and behavioural ecology of free-living sea turtles; long-term monitoring of populations is revealing conservation concerns as well as conservation success stories, and key remaining issues related to the biology and conservation of this group are now starting to clearly crystallise. This special issue celebrates some of these areas of development. In this review I take a journey through some of these recent discoveries and highlight some of the topics that are expected to be attracting increasing interest in coming years.

## 2. Energetic budgets

At the heart of the life history of all animals is their metabolic rate, which combines with ingestion rates to influence the overall energy budget for an animal. In this issue [Wallace et al. \(2008-this issue\)](#) review our knowledge of sea turtle metabolic

rates. Sea turtles, being reptiles, are largely considered to be ectothermic and, consequently, to have a low metabolic rate. This view has been confirmed with energy expenditure values measured via respirometry both in the laboratory and on nesting beaches. The consequences of this low metabolic rate is that turtles use their energy reserves very slowly and can consequently survive very long periods of fasting associated with long distance migration. For example, [Fig. 1](#) shows the trajectories of body mass changes for green turtles (*Chelonia mydas*) and elephant seals (*Mirounga angustirostris*) fasting during the breeding season. Being endothermic the seal loses mass at a much greater rate when fasting and, consequently, needs a larger relative energy store to sustain itself during the breeding season. However, while there has been little controversy regarding the metabolic rate for most species of sea turtles, the metabolic rates of leatherbacks (*Dermochelys coriacea*) has long been debated. The leatherback turtle has the greatest range of any sea turtle species with adults routinely being found at high latitude during the summer (e.g. [James et al., 2006](#); [Houghton et al., 2006](#)). Fuelled by observations that individuals swimming in cold, high latitude water could have elevated body temperatures ([Frair et al., 1972](#)), there was the suggestion that leatherbacks might have high, non-ectothermic, metabolic rates, to fuel these warm body temperatures ([Paladino et al., 1990](#)). The debate has been prolonged because of the difficulties of measuring the metabolic rate of adult

*E-mail address:* [g.hays@swan.ac.uk](mailto:g.hays@swan.ac.uk).

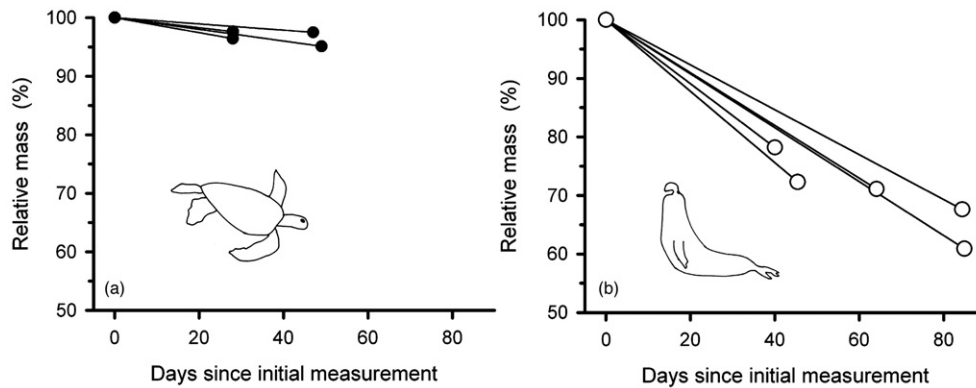


Fig. 1. Mass loss for (a) green turtles (*Chelonia mydas*) and (b) elephants seals (*Mirounga angustirostris*) during the breeding season at sites where individuals fast. The green turtle data are for females at Ascension Island, a major breeding site that is very distant from the population foraging grounds along the South American coast (Hays et al., 2002). The elephant seal data comes from California (Deutsch et al., 1990). Each line connects the mass for the same individual with initial mass scaled to 100%. Mass loss trajectories are representative of the data from much larger sample issues in the original papers, but only a few individuals are shown here for clarity. The much larger mass loss in the fasting endotherm (seal) compared to the fasting ectotherm (turtle) is clearly evident.

leatherback turtles. However, recently two approaches have been used to get to the bottom of this problem. Wallace et al. (2005) successfully used doubly labelled water to estimate the metabolic rate of free-living leatherbacks, while Bradshaw et al. (2007) used dive data relayed from free-living individuals to define their aerobic dive limit which, when combined with knowledge of their oxygen stores, could be used to estimate their diving metabolic rate. Despite limitations with both techniques, they both gave a predominant view that leatherback turtles are ectothermic and have a low reptilian metabolic rate when compared to endotherms of equivalent size. This low metabolic rate presumably allows leatherbacks to survive on their diet of gelatinous zooplankton which have a low energy density (Doyle et al., 2007). The warm body temperature reported for leatherback turtles in cold water therefore might stem simply from their large body size, and resulting thermal inertia, combined with insulation and heat exchangers to reduce heat loss. In addition, it has been suggested the leatherbacks might swim more actively in cold water to generate more heat (Bostrom and Jones, 2007) although this idea has yet to be tested.

A challenging objective for future research will be to complete robust energy budgets for species such as leatherback turtles that combine information on their metabolic rate, energy density of prey and ingestion rates to assess energy balance over long periods, ideally the several years between successive breeding seasons. Such energy budgets may explain the drivers of differences in the periodicity of nesting both between species and between populations (Broderick et al., 2001). Establishing the energy budgets for sea turtles also impinges on their conservation ecology as reproductive output is fundamentally linked to the balance between energy expenditure and energy intake, with individuals probably requiring some threshold body condition before they can return to breed (Hays 2000; Alerstam et al., 2003). The question is particularly relevant in the case of establishing the underlying reasons for the differences in conservation status of leatherback turtles in the Pacific versus Atlantic basins. Despite a high risk of bycatch in fisheries in both ocean basins, as highlighted in this issue by Fossette et al. (2008-this issue) there are

large numbers of leatherback turtles in the Atlantic and populations seem to be largely stable or increasing in size. In contrast there have been very heavy declines in leatherback numbers in the Pacific. Presumably linked to this Atlantic versus Pacific difference in conservation status, is the fact that the interval between consecutive breeding seasons is lower in the Atlantic (typically two or three years) compared to the Pacific (typically four or five years). These marked differences in the ecology and conservation status of leatherbacks in the Atlantic versus Pacific point to differences in the prey fields of these ocean basins with presumably higher prey abundance in the Atlantic (Wallace et al., 2006). Completing robust energy budgets for these leatherbacks in these ocean basins will therefore be an important step in identifying the underlying reasons for the different trends in population sizes.

### 3. Movement analysis: identifying foraging hotspots and animal state

The last decade has seen a rapid increase in the number of tracking studies both with sea turtles and a range of other marine vertebrates such as birds, mammals and fish. Across this range of taxa a variety of tracking technologies have been used ranging from archival tags that measure light intensity allowing light based geolocations with a typical accuracy of the order of 100 s of kms, to Argos satellite tracking which typically offers a resolution of a few kms, to GPS tracking which provides resolution of few 10 s of metres (Ryan et al., 2004; Bradshaw et al., 2007). For many species very broad scale oceanic movements have been identified (Fig. 2). For example elephants seals; (Biuw et al., 2007), leatherback turtles (Hays et al., 2006; Eckert, 2006; Benson et al., 2007), bluefin tuna (Block et al., 2005; Schick et al., 2004) and shearwaters (Shaffer et al., 2006) to name but a few have all been tracked moving 100 s or 1000 s of km across ocean basins. A key focus from such data-sets, both for sea turtles and other taxa, is to objectively identify areas of high use (e.g. Worm et al., 2003; James et al., 2005; Eckert 2006). Identifying these “hotspots” is important for a number of reasons. First hotspots may

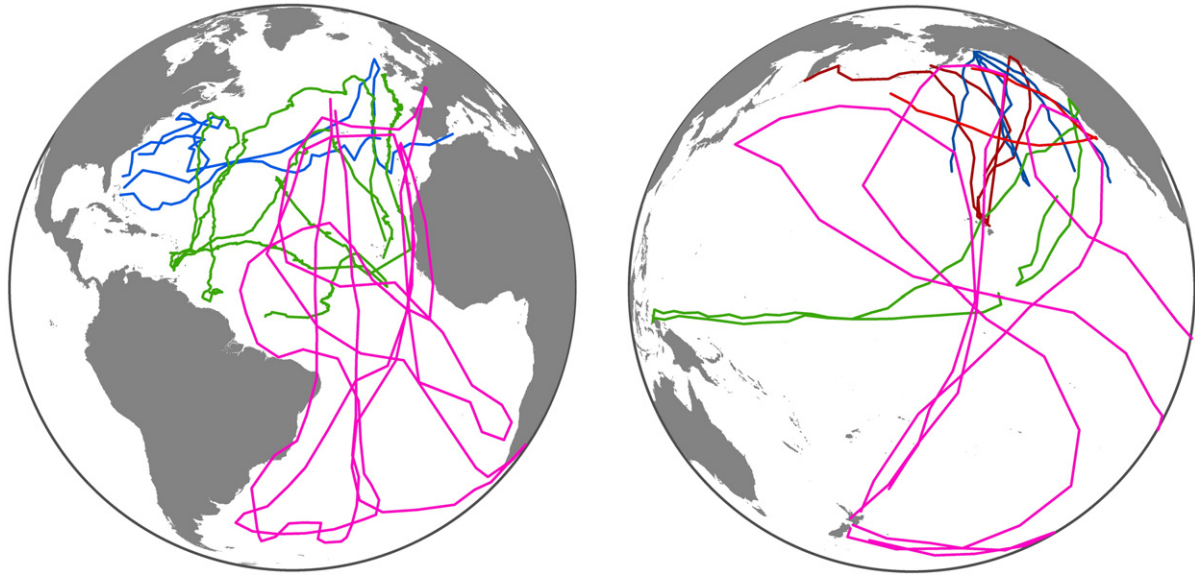


Fig. 2. Tracks obtained with data-loggers and transmitters attached to various marine species. Atlantic: bluefin tuna (blue lines), leatherback turtles (green lines) and petrels (pink lines). Pacific: leatherback turtles (green lines), salmon sharks (blue lines); shearwaters (pink lines), humpback whales and elephant seals (red lines). Tracks adapted from Benson et al. (2007), Block et al. (2005), González-Solís et al. (2007), Hays et al. (2006), Le Boeuf et al. (2000), Mate et al. (2007), Shaffer et al. (2006) and Weng et al. (2005). Despite the broad range of species and tracking technologies employed, pervading across these types of study is the question of what determines how animals move through their environment and find prey that are patchily distributed. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

play a central role in the foraging ecology and annual energy budget of individuals. For example, using a sea turtle example, results from leatherbacks have shown that individuals may spend relatively little time in zones where they travel slowly and exhibit localised area restricting searches (Hays et al., 2006; Jonsen et al., 2007). However, these small periods presumably play a large role in dictating the overall annual energy intake for individuals, since we know that their zooplankton prey are very patchily distributed in oceanic environments and may be found in localised, but rare, very high abundance patches (Houghton et al., 2006). Identifying the underlying search rules that animals employ to find these hotspots is therefore a fundamental question pervading across species boundaries. As well as a fundamental interest in foraging ecology, hotspot identification is also important in efforts to protect sea turtles from incidental bycatch (Ferraroli et al., 2004). Bycatch in pelagic longlines and gillnet fisheries has been identified as an important source of mortality for pelagic turtles in a variety of ocean basins (Lewison et al., 2004). The intensity of fishing effort in the open ocean is staggering with, for example, estimates that the density of longlines hooks may be over 10 million per 5° by 5° area per year in intensely fished areas (Lewison et al., 2004). Clearly hotspots that animals target may be important sites to focus conservation efforts.

There are at least four approaches to help achieve the goal of understating what drives the movements of animals foraging in the open ocean: improved resolution of tracking; using additional behavioural information, such as dive data, to inform on the state of an animal (e.g. travelling versus foraging); improved use of environmental maps of the areas around animals; improved data processing using various quantitative movement analyses. In this special issue several of these approaches are developed. Kobayashi et al. (2008-this issue) reveal long-term oceanic tracks

for 186 loggerhead turtles tracked in the North Pacific which are quantitatively compared to various environmental maps, some derived from satellite remote sensed imagery. Kobayashi et al. (2008-this issue) illustrate how sea surface temperature and chlorophyll help to explain where pelagic loggerheads are found, with these variables being used to identify the Transition Zone Chlorophyll Front (TZCF), a basin-wide frontal feature that delineates warm, vertically stratified, low surface chlorophyll-a water of the subtropical gyre from the vertically mixed cool, higher surface chlorophyll-a Transition Zone. Elsewhere in this issue Bailey et al. (2008-this issue) develop the use of state-space models for identifying the switches in state of leatherback turtles in the Pacific between their reproductive interesting state to their post-nesting travelling stage and their restricted area search foraging state in the open ocean. State-space models form one of the quantitative movement analysis tools increasingly being used to process tracking data sets (Jonsen et al., 2006). In common with other approaches such as step-length analysis, fractal analysis and first passage time analysis, these statistical tools all endeavour to objectively define and delineate what animals are doing along different parts of their tracks and we can expect that these approaches will gradually replace more subjective analysis of tracks. These techniques hold great promise for quantifying differences in behaviour by turtles in different parts of their range as well as identifying population differences in behaviour, such as the case of leatherback turtles in the Atlantic and Pacific (see Section 2).

#### 4. Free-living behaviour determined with data-loggers

As well as widespread deployment of satellite tags to track various marine vertebrates, the last decade has also seen widespread

use of data-loggers to record the diving behaviour of a wide range of species, with some of these units indeed being linked to satellite transmitters (e.g. [Biuw et al., 2007](#); [Sims et al., 2005](#)). These devices have quantified a number of aspects of turtle dive performance. In the case of sea turtles, individuals of some species (e.g. green turtles, loggerhead turtles and hawksbill turtles) have been shown to rest on the seabed for long periods at night, with typical dive durations in the order of 45 min (e.g. [Houghton et al., 2002](#)), while during the winter they have been shown to stay submerged for exceptionally long periods (many hours), sometimes surfacing only three or four times a day ([Hochscheid et al., 2005a, 2007](#)). These dives are thought to be aerobic with the long dive duration been explained by low metabolic rates at low temperatures. As well as incredibly long dives, dive sensors have also revealed very deep dives, with leatherbacks now been recorded to dive over 1200 m ([Fig. 3](#)) ([Doyle et al., in press](#)).

To date deployment of data loggers on sea turtles has generally been constrained to the interesting period when the repeated emergence of females to nest allows for instrument deployment and recovery. For dive sensors linked to satellite tags the standard deployment is on females at the end of the nesting season to record their postnesting behaviour. It is much more difficult to record the dive behaviour of turtles on their way travelling from foraging grounds to nesting beaches. The difficulties lie in knowing when a turtle will make this journey, as well as capturing such turtles for instrument attachment. Set against this backdrop, in this issue [Rice and Balazs \(2008-this issue\)](#) present results from a serendipitous study in which dive recorders were attached to green turtles at their foraging grounds in Hawaii just before several individuals travelled back to their nesting beaches. The resulting dive data sets are unique and reveal a complexity to dive performance during migration. During the day turtles seem to travel mainly close to, but not at the surface, consistent with considerations that sub-surface travel will minimise the cost of travel. However at night, turtles conducted deeper dives involving an initial deep descent following by a gradual midwater ascent. The function of these dives, originally described in sea snakes

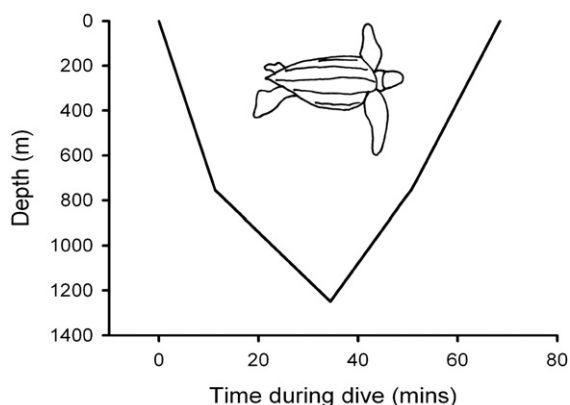


Fig. 3. Record breaking. A dive to 1250 m made by a leatherback turtle near the Cape Verde Islands (north Atlantic), the deepest dive profile so far obtained from a sea turtle (reported in [Doyle et al., in press](#)). Literally hundreds of thousands of dive profiles have now been recorded for various species of sea turtle as well as marine mammals and birds. A key focus now is to establish the function of different dive types.

([Graham et al., 1987](#)), remains enigmatic, although they might at least partly involve turtles searching for the seabed. Certainly we know that when given the chance green turtles normally chose to rest on the seabed and indeed for turtles migrating back to their nesting beaches, [Rice and Balazs \(2008-this issue\)](#) were clearly able to show when turtles arrived at their nesting grounds due to the switch to U-shaped benthic, presumably resting, dives. Such U-shaped dives are now well described in sea turtles. The lack of variation in the bottom phase has been used to infer a function of benthic resting and indeed direct observations by divers have shown turtles rest on the seabed. Moreover, data loggers have recently been developed that can directly record the state of consciousness of turtles ([Hochscheid et al., 2005b](#)). By attaching a motion sensor to the mouth of captive loggerhead turtles, [Hochscheid et al. \(2005b\)](#) measured rhythmic movement of the throat region, termed buccal oscillations, when turtles were awake, probably reflecting the turtles smelling the water for potential prey and predators. The motion sensors have recently been attached to free-living turtles and the data collected shows the same patterns of turtles sleeping on the sea bed during long U-dives ([Houghton et al., 2008-this issue](#)).

This work by [Houghton et al. \(2008-this issue\)](#) forms part of a general thrust among behavioural ecologists to supplement information on animal dive profiles, which are now relatively easy to measure, with more information on exactly what behaviours animals are performing during dives. For example devices are now being deployed that measure feeding attempts and flipper or fin beats (i.e. swimming effort) on animals as diverse as sperm whales, seals and turtles (e.g. [Austin et al., 2006](#); [Hays et al., 2004](#); [Watwood et al., 2006](#); [Wilson et al., 2002](#)). Other data-loggers offer the possibility of measuring the instantaneous metabolic rate of free-living animals, including marine vertebrates ([Butler et al., 2004](#); [Wilson et al., 2006](#)). We can see ever increasing use of advanced data loggers such as these to shed further light on the function of different dive types, with even more linkage between what can be recorded by data-loggers and what can be relayed remotely (e.g. via satellite).

## 5. Impact of predation

To date most work with tracking turtles, as well as marine mammals, fish and birds, has tended to couch the movements exhibited in terms of resource acquisition (foraging) and reproduction (e.g. travel to breeding sites). For example bluefin tuna are thought to move between spawning grounds in the Gulf of Mexico and disparate foraging grounds in the Atlantic ([Block et al., 2005](#)). Likewise leatherback turtles move across the entire width of the north Atlantic in search of their gelatinous zooplankton prey ([Eckert 2006](#); [Hays et al., 2006](#); [Jonsen et al., 2007](#)). However, there are now inklings that the risk of predation may play an important role, aside from reproduction and foraging, in driving the pattern of movements ([Heithaus et al., 2008-this issue](#)). For example, [Heithaus et al. \(2007\)](#) have shown how green turtles can trade off a high risk of predation with foraging success. In the aptly named Shark Bay, Australia, green turtles live in an environment where areas of good foraging (abundant sea grass) correspond with areas where the risk of predation from tiger

sharks is high; while areas of lower predation risk have poor food availability. Heithaus et al. (2007) showed how animals in good body condition seem to forgo the good foraging sites, with the maxim being “better hungry than dead”. Only those individuals in poor condition are forced to undergo the gauntlet of high predation risk in search of food. Interestingly this same trade off between food availability and predation risk has been shown in invertebrates such as copepods (Hays et al., 2001), suggesting that predation risk may shape patterns of habitat utilisation by a broad range of animals. However, studies with marine vertebrates such as those of Heithaus et al. (2007) are rare. Yet presumably predation risk plays important roles in structuring the pattern of both horizontal and vertical movement of a broad range of marine vertebrates.

## 6. Concluding remarks

In this review I have highlighted some of the topical areas for sea turtle research. However, my coverage is far from complete and even in this special issue there is reference to many other developments in the field of sea turtle biology and conservation. Lohmann et al. (2008-this issue) review the state of knowledge concerning the mechanisms used in long distance migration by sea turtles. Long considered accomplished ocean migrants able to find distant remote targets, the field of sea navigation has benefited hugely in recent years from the combination of elegant laboratory experiments to tease apart the sensory capabilities of sea turtles, along with field experiments in which turtles have been manipulated to test their navigational skills under various scenarios. Interestingly it has been shown the turtles cannot always locate distant targets, i.e. even for these accomplished travellers there are limits to their ability. For example sea turtles displaced from Ascension Island have been shown to often have difficulty in relocating the island (Luschi et al., 2001). Merging laboratory and field investigations into a unified view of sea turtle navigation is now an attainable goal and is likely to benefit from the improvements in tracking technology that allow animals to be followed with finer scale resolution (e.g. Schofield et al., 2007).

Also covered in this special issue are the developments in the use of molecular tools to explore aspects of sea turtle ecology (Lee, 2008-this issue). Most recently molecular tools have been used to assess small scale fidelity of both male and female turtles to particular nesting beaches (Lee et al., 2007), patterns of multiple paternity both within and across populations (Moore and Ball, 2002; Lee and Hays, 2004; Jensen et al., 2006) and the links between the occurrence of juvenile turtles on foraging grounds and potential source rookeries, sometimes thousand of kms distant (Bowen et al., 1995; Bass et al., 2006).

One topic that may increasingly dominate sea turtle studies is the implications of climate change. Climate change may have a number of profound impacts on sea turtles such as altering the timing of the nesting season (i.e. phenology) and species distributions (e.g. Weishampel et al., 2004). Long-term data-sets will be increasingly important in detecting these changes. In this special issue Chaloupka et al. (2008-this issue) examine several multi-decadal data sets on nesting numbers for loggerhead turtles from various sites in Pacific. Despite contrasting long-term trends

in nesting numbers, Chaloupka et al. (2008-this issue) reveal that across rookeries there is a consistent role of sea surface temperature (SST) in influencing nesting numbers. Most probably this SST-nesting numbers link is mediated through SST influencing feeding conditions and hence the remigration rate for individuals (Hays, 2000). A vital focus for future studies will be both to identify and predict the impacts of climate. As Chaloupka et al. (2008-this issue) point out, a worst case scenario is that warming temperatures may lead to some sea turtle populations becoming regionally extinct. This scenario will pose huge questions for the conservation management of populations.

Finally in work that is hugely important for sea turtle conservation, Seminoff and Shanker (this issue) review the IUCN listings for sea turtles. There has been extended recent debate over the use and misuse of these listings with the pervading view being that the listings may sometimes give an overly pessimistic view of the status of populations. For example, species listed as critically endangered may in fact, not be close to the formal definition of this designation (“imminent risk of extinction”). For example, leatherback turtle numbers in the Atlantic are relatively healthy (Fossette et al., 2008-this issue). Similarly green turtles are listed as endangered, but again many populations are doing well (e.g. Godley et al., 2001). The problem arises in that if the IUCN listings are not accurate in all instances, then they may be devalued and divert conservation attention away from where it is really needed. What is clear is from the review provided by Seminoff and Shanker (2008-this issue) is the widespread acceptance that the current IUCN listings are not ideal and therefore a pressing challenge will be to produce a better system that achieves its ultimate goal of identifying those species and populations of most pressing conservation concern.

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