

Thermal niche, large-scale movements and implications of climate change for a critically endangered marine vertebrate

CLIVE R. McMAHON and GRAEME C. HAYS

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

Abstract

Climate change is expected to have a number of impacts on biological communities including range extensions and contractions. Recent analyses of multidecadal data sets have shown such monotonic shifts in the distribution of plankton communities and various fish species, both groups for which there is a large amount of historical data on distribution. However, establishing the implications of climate change for the range of endangered species is problematic as historic data are often lacking. We therefore used a different approach to predict the implications of climate change for the range of the critically endangered planktivorous leatherback turtle (*Dermochelys coriacea*). We used long-term satellite telemetry to define the habitat utilization of this species. We show that the northerly distribution limit of this species can essentially be encapsulated by the position of the 15 °C isotherm and that the summer position of this isotherm has moved north by 330 km in the North Atlantic in the last 17 years. Consequently, conservation measures will need to operate over ever-widening areas to accommodate this range extension.

Key words: bycatch, conservation, leatherback turtle, longline, range expansion

Received 13 July 2005; revised version received 12 January 2006; accepted 19 January 2006

Introduction

Over the past 100 years, the global average temperature has increased by approximately 0.6 °C, and it is now widely accepted that this warming trend will continue, but how this warming affects the world's oceans remains unclear (Edwards & Richardson, 2004; Richardson & Schoeman, 2004). What is clear is that the distribution of some organisms can be a sensitive indicator of climate change (Hughes, 2000). Range extensions in terrestrial systems in response to climate warming are widely documented (Parmesan & Yohe, 2003; Root *et al.*, 2003), but some striking examples also exist in ocean plankton (Beaugrand *et al.*, 2002) and marine fish (Perry *et al.*, 2005). There is, for example, evidence of increased occurrence of 'exotic' species of fish in UK waters (Stebbing *et al.*, 2002), as well as changes in species distribution and composition (Gerner *et al.*, 2004). However, it can be difficult to observe directly the movements of marine animals in relation to

physical features such as water temperature and thereby show a direct causal link between thermal conditions and species range. For example, range expansions by predators may be the result of prey redistributions and the shifts in range may be a response to the prey movements rather than directly to temperature. However, for larger vertebrates it is possible to directly track movements (e.g. Metcalfe & Arnold, 1997; Luschi *et al.*, 2003) and so empirically establish how environmental conditions shape distribution, allowing objective predictions to be made regarding the implications of climate change.

Establishing such links for endangered animals is especially difficult because access to animals can be restricted or only few animals may be available for study, which needless to say limits the power associated with such studies. However, such limitation need not dictate whether animals are studied or not because life-history information, even that gathered from a few individuals, may be crucial to conservation and management. Hence, the fact that few animals may be available should not preclude them from study (Caughley & Gunn, 1996). Indeed, it is imperative that critically

Correspondence: Graeme C. Hays, tel. +44 (0) 1792 295375, fax +44 (0) 1792 295447, e-mail: g.hays@swansea.ac.uk

endangered animals be studied while they can, i.e. before they become extinct, so that informed management decisions can be made.

Because of the availability of spatially and temporally extensive plankton abundance data-sets, such as those provided by the Continuous Plankton Recorder Survey (Warner & Hays, 1994), the North Atlantic provides a useful general area for disentangling the impacts of prey fields and temperature in driving possible range extensions of planktivores. Indeed, even with small sample sizes, informative studies of the physiological ecology of planktivorous vertebrates are now starting to be made (Sims *et al.*, 2005). We therefore set out to establish the relative roles of food availability and water temperature in dictating the northerly distribution of critically endangered leatherback turtles (*Dermochelys coriacea*). By combining information on the thermal properties of the leatherback turtle's habitat with the general availability of food, we set out to describe the factors which are most likely to explain the distribution of this species. In effect, we try to identify the 'climate envelope' that encompasses the range of this species, an approach that is particularly useful when limited data are available (Pearson & Dawson, 2003). This approach is important for endangered species as it will provide guidance on where future conservation measures need to be directed.

Methods

Satellite tracking

To record the movements of leatherback turtles we attached satellite transmitters (Satellite Relay Data Loggers [SRDLs] manufactured by the Sea Mammal Research Unit, St Andrews, UK) to adult female turtles nesting at Levera beach on the north shore of Grenada, Caribbean (12.2°N, 61.6°W) (Hays *et al.*, 2004). We only tracked females because they are more accessible than male turtles on breeding beaches, but it should be noted that our results may be equally applicable to males as there is no detectable gender difference in the at-sea behavior of female and male leatherback turtles (James *et al.*, 2005).

The location of transmitters was determined using the Argos system, which assigns a level of accuracy to each location. Based on previous trials of location accuracy (Hays *et al.*, 2001; White & Sjoberg, 2002) we generally used only locations of the best four classes (location classes 1, 2, 3 and A) when reconstructing the migration tracks. The exception to this rule was on rare occasions when there was >7 days between these high-quality locations and in these instances we used locations of classes 0 and B. Locations were then filtered to

remove those locations which necessitated a speed of travel of $>9\text{ km h}^{-1}$ between consecutive locations $>30\text{ km}$ apart.

Dive information

Each SRDL contained a pressure sensor, which measured depth to an accuracy of 0.33 m every 4 s. Individual dives were recorded when the water depth exceeded 10 m. Once a dive was completed, on-board software examined the dive profile and determined the time and depth of the five most significant points of inflexion during the dive. The time and depth of these five points along with the time of the end of the dive and dive duration were then transmitted. Each dive entered a buffer within the SRDL, so that these data would be randomly transmitted for the next 10 days ensuring that the specific dive profiles obtained via the Argos system were not weighted by the surfacing behavior of the turtle. The SRDL also summarized the dive information into 6 h summary periods. Included in the parameters determined for each summary period was the percentage time spent deeper than 10 m and the mean depth of dives to $>10\text{ m}$. In addition, the maximum depth ever recorded by each SRDL was transmitted regularly.

Temperature measurements

To compliment their primary function of gathering data about turtle migratory and diving behavior, the SRDLs were also programmed to record temperature upcasts on the deepest dive in each 12-h period (provided that the dive reached a depth of at least 25 m). Temperature and pressure were sampled at 1 Hz and the results averaged into 1 dbar bins (1 dbar increase in pressure is equivalent to approximately 1 m of seawater). These raw data were then processed according to the method used for XBT floats: that is, a five-point median filter was applied to remove outliers, followed by a Hanning filter (Orstom, 2000). Twelve depth-temperature points were then selected to approximate the cast by the broken-stick algorithm, and these coordinates were encoded along with a timestamp to fit in a single 31-byte message. The resulting data string was stored in a buffer where it was made available for transmission for up to 5 days. The SRDL is highly configurable: in particular, it allows priorities to be assigned to the various data types that it collects, reflected in the volume of each type that it transmits. In this case, temperature casts represented 12.5% of the transmissions made by the SRDL. We have shown that these temperature data provided by SRDLs remain robust and subject to little drift even during long-term deployments (McMahon *et al.*, 2005).

To quantify the leatherback turtle thermal habitat we calculated the mean weekly temperature from the SRDLs for each of the seven turtles tracked in 2003/2004 (Fig. 1, turtles C–I). When temperature data were not available from the SRDLs but positions were known, we used the mean sea surface temperatures (SSTs) from the geo-referenced SST AVHRR Pathfinder data (see below for details). To assess the thermal habitats encountered by the two (A and B) turtles tracked in 2002/2003, weekly SSTs were calculated from data supplied by ICOADS (Diaz *et al.*, 2002). To assess the SST around the United Kingdom we used monthly

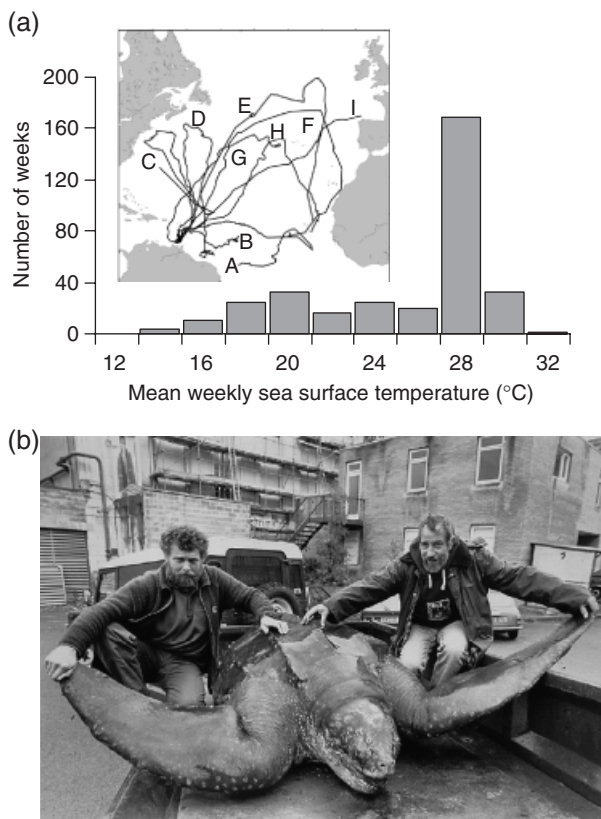


Fig. 1 (a) The range of sea surface temperatures (SSTs) encountered by nine satellite tracked leatherback turtles. Inset shows the pan-oceanic migrations for the nine turtles tracked from their breeding grounds in the west tropical Atlantic Ocean, updated from Hays *et al.* (2004) to include all tracking data before the transmitters failed. Main panel shows the SSTs. For seven of the turtles (C–I), which relayed water temperature data, we calculated the mean weekly temperature in the top 20 m of the water column. For two turtles (A and B) not equipped with temperature recording Satellite Relay Data Loggers, the weekly mean SSTs was derived from ICOADS. Overall <2% of the total time was spent where SST was below 15 °C. Further evidence of the northerly migrations of leatherback turtles are evident in the occurrence of (b) stranded leatherback turtles such as this turtle washed up on a beach in North Wales, UK.

data from the Hadley Centre of the UK Met Office (HadISST) for the geographical area bounded by 45–60°N and 0–15°W and for the years 1970–2003. The ICOADS and HadISST data sets are essentially US and UK products, respectively, that use much of the same data derived from a combination of ship measurements, as well as those from moored and drifting buoys. We simply used those products readily available for those areas of interest, using ICOADS for basin wide temperature data and HadISST for data from around the United Kingdom.

The latitudinal position of the 15 °C isotherm was located at 5° longitude intervals from 5°E to 70°W from the geo-referenced SST AVHRR Pathfinder data supplied by Plymouth Marine Laboratory as part of the NERC Remote Sensing Data Analysis Service.

Zooplankton biomass

To describe the role that food availability may have on the seasonal occurrence of leatherback turtles in the United Kingdom and Ireland, we used the integrated results on seasonal zooplankton biomass in the Celtic Sea, south-west of the United Kingdom, provided by combining results from continuous plankton recorder (CPR) and Longhurst–Hardy plankton recorder (LHPR) data (Batten *et al.*, 1999). These two samplers provide an unprecedented series of samples on the near surface (CPR) and depth-related (LHPR) zooplankton abundance and hence in combination provide a very robust measure of seasonal zooplankton abundance. We use these data because it is well known that leatherback turtles are planktivorous, albeit on gelatinous zooplankton such as scyphozoan jellyfish and pyrosomes (Davenport, 1998) for which little or no data exists on seasonal patterns of abundance. We, therefore, use overall zooplankton abundance as sampled by CPRs and LHPRs (generally crustaceans) as the best-available proxy for the seasonal abundance of gelatinous zooplankton.

From Batten *et al.* (1999) we digitized Fig. 3 and combined zooplankton abundance estimates from both off the continental shelf and on the shelf within the Celtic Sea. As turtles generally restrict their diving to the top 50 m at high latitudes (McMahon *et al.*, 2005), we calculated the depth-integrated biomass for each month for the top 50 m of the water column.

It should be noted that within CPR samples the presence or absence of jelly-like material is recorded within the category 'coelenterate tissue' (Warner & Hays, 1994). However, whether these qualitative assessments provide a real indication of the abundance of gelatinous zooplankton is unknown. More detailed analysis of archived CPR samples is possible, for

example, using nematocysts to positively identify jellyfish. Such studies should be encouraged, as the CPR survey data could potentially provide data on seasonal and spatial patterns of gelatinous zooplankton, albeit only at a fixed near surface depth.

Turtle numbers in the United Kingdom and Ireland

To examine the seasonal pattern of leatherback occurrence around the United Kingdom and Ireland we used the database, TURTLE. This includes information published in popular accounts and the scientific literature, as well as unpublished reports and presents turtle records in a standard, digital format (<http://www.strandings.com/Wales.html>). To examine leatherback seasonality, we used only records of live sightings, as it is known that dead animals may strand long after dying (Pierpoint, 2000).

Turtle numbers at higher latitudes

To provide a comparable index of turtle numbers throughout northern Europe we used the data set assembled by Brongersma (1972). Brongersma (1972) compiled leatherback turtle records not only for the United Kingdom but also further north, such as Iceland and Norway. This geographically broad data set has not been subsequently updated (the TURTLE database outlined above has a United Kingdom and Ireland focus) and so provides the best currently available comparable measure of the relative abundance of leatherbacks in the United Kingdom vs. more northerly latitudes.

Results

In 2002/2003, two leatherback turtles were tracked for 333 and 376 days (A and B, respectively, Fig. 1a), between July 2002 and July 2003 as they moved from their nesting ground in the Caribbean. These two turtles remained in warm waters that were on average 26.8 °C (20–32.4 °C) at the surface. These turtles did not spend any time in surface waters cooler than 20 °C and concentrated their movements in a relatively narrow band between 20 and 60°W and 03 and 20°N (Fig. 1a). In 2003/2004, a further seven leatherback turtles (C–I in Fig. 1) were tracked for a total of 2434 days (minimum 182 days and maximum 432 days) between April 2003 and September 2004 from their nesting grounds in the Caribbean. These seven turtles moved across the entire North Atlantic Ocean basin between 05 and 75°W and 05 and 55°N (Fig. 1a) where the sea surface temperatures, measured *in situ* by the SRDLs the turtles were equipped with, varied between 13.3 and 28.5 °C (mean 24.8 °C, $n = 4430$ temperature/depth readings). Three

turtles (C, D and H in Fig. 1a) traveled to areas where SSTs were below 18 °C (i.e. in the lower quartile of the observed temperature range) and all displayed similar behavior patterns in that they all switched from traveling in a general northerly direction to traveling in a southerly direction when they encountered temperatures between 12 and 18 °C. Turtles spent very little time (2%) in areas where the surface waters were below 15 °C (Fig. 1). This suggests that a water temperature around 15 °C may represent a thermal constraint on the northerly movements of leatherback turtles.

Turtles generally conducted deeper dives when the surface water was warmer (Fig. 2). Consequently, rela-

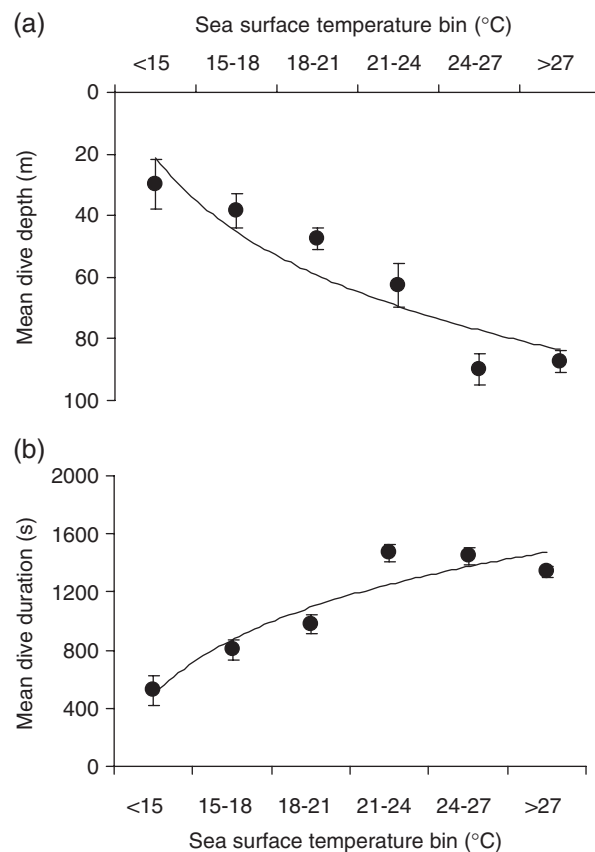


Fig. 2 The diving behavior of leatherback turtles ($n = 7$) was affected by the temperature recorded at the surface, so that (a) mean dive depths ($\pm 2SE$) were shallower in colder waters than in warmer waters and (b) dive durations ($\pm 2SE$) were shorter in colder waters than in warmer waters. The curvilinear relationships were highly significant ($P < 0.01$ in both cases) and sea surface temperature explained the majority of the variation in dive depth and dive duration ($r^2 = 0.84$ and 0.87 , respectively). For our comparison here we used the concurrent temperature depth data collected for the seven leatherback turtles which carried instruments where both data recordings were made. The surface temperatures represented here are the mean temperatures in the top 20 m of the water column associated with individual dives.

tively cold subsurface water could be encountered even when surface waters were relatively warm (Fig. 3). The coldest relayed temperature that the turtles in this study encountered was 9.48 °C, which occurred at a depth of 438 m in the tropical Atlantic Ocean.

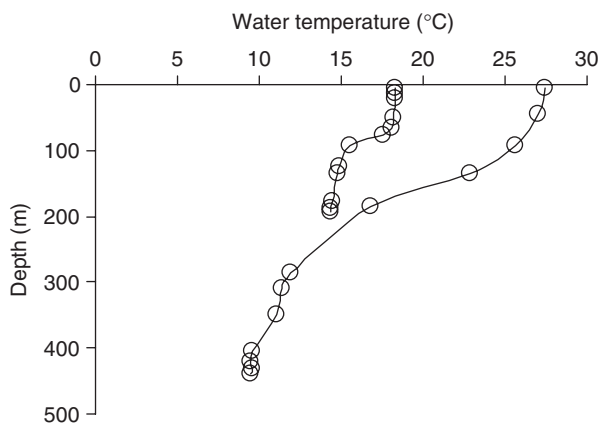


Fig. 3 Examples of the temperature–depth profiles that were relayed via the Satellite Relay Data Loggers showing how relatively cold temperatures could be experienced on deep dives where surface waters were relatively warm.

Leatherback turtles appear to restrict their oceanic distributions to areas south of the 15 °C isotherm (i.e. surface water warmer than 15 °C), which places the United Kingdom near the northern limits of their range. The United Kingdom is, therefore, an ideal location from which to monitor range extensions and assess habitat preference. We noted that the 15 °C isotherm was a dynamic ocean feature (Fig. 4) which showed extremes in average extent so that in 2000 the isotherm occurred furthest north (Fig. 4b) and in 1985 it was displaced furthest south (Fig. 4a). However, there has been a general northerly movement of the isotherm since 1983. For example, the mean position of the 15 °C isotherm (assessed between 5°E and 70°W) has moved north by 3° of latitude (approximately 330 km over 15 years) (Fig. 4c).

A total of 421 (301 alive and 120 dead) leatherback turtles were reported in seas surrounding the United Kingdom between 1985 and 2002. Live sightings peaked in August when mean monthly sea surface temperatures were warmest (Fig. 5b). Temperature may not be the only factor that describes the distribution or occurrence of leatherback turtles in the northern Atlantic: food may potentially be a contributor. However, we

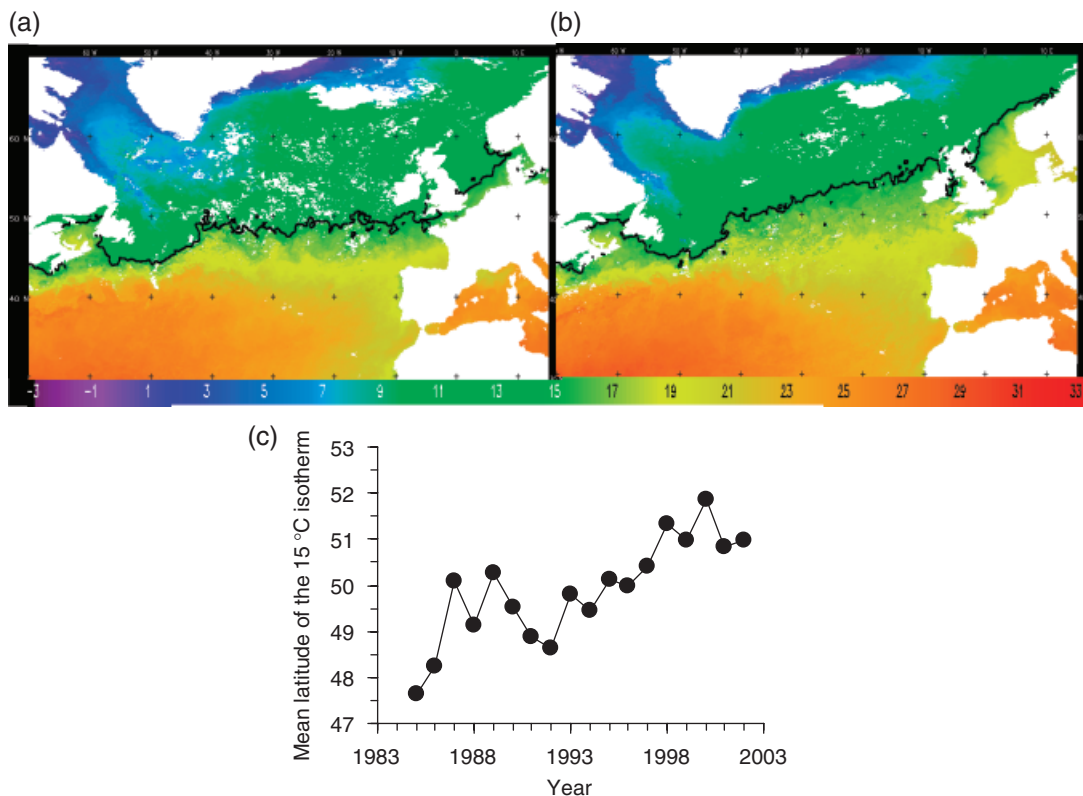


Fig. 4 The position of the 15 °C surface isotherm in different years. (a, b) AVHRR Satellite images comparing years when the position of this isotherm in August was at its most southerly extent (1985) and most northerly extent (2000). (c) The increasing northerly extent of the surface 15 °C surface isotherm in August (error bars ± 2 SE are smaller than the plot symbols), showing a northerly shift of 330 km over recent years.

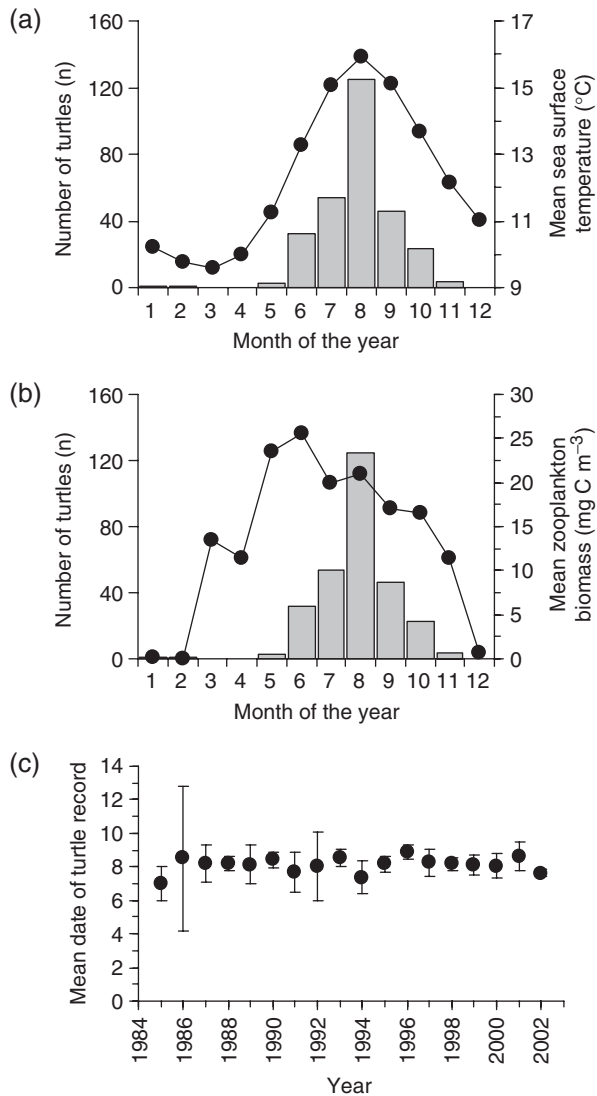


Fig. 5 The seasonality of leatherback turtle occurrences in United Kingdom and Irish waters (a, b) the number of live leatherback sightings in each month alongside the mean sea surface temperature (error bars $\pm 2SE$ are smaller than the plot symbols) around the United Kingdom and zooplankton biomass (in mg carbon m^{-3}) in the Celtic Sea, respectively. (c) The annual midpoint of live leatherback sightings in different years ($\pm 2SE$), showing the consistent pattern for maximal occurrence in August.

found that while zooplankton biomass varied seasonally, there was an extended seasonal peak in biomass that lasted from April to October (Fig. 5b). To confirm which of our *a priori* predictors was the best descriptor of turtle numbers, we performed a stepwise regression analysis of monthly turtle numbers vs. both water temperature and zooplankton abundance. Water temperature was the only significant predictor of turtle numbers ($r^2 = 0.71$). The peak in the number of leather-

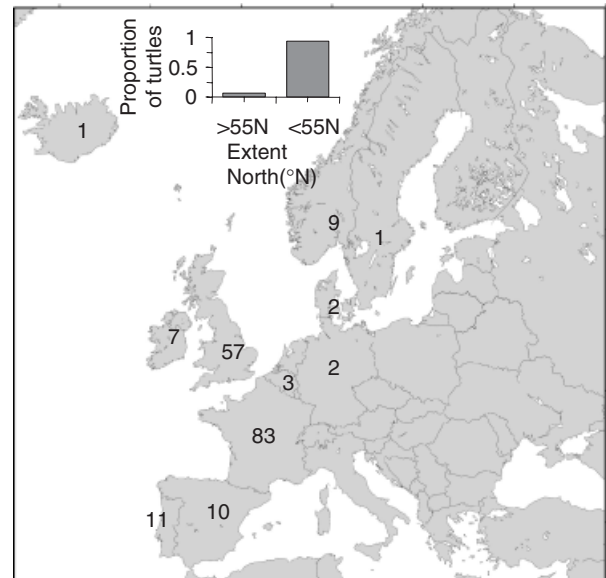


Fig. 6 A summary of the numbers of leatherback turtles recorded in the North Atlantic compiled by Brongersma (1972), showing that while leatherback turtles have been seen at very high latitudes, such as Iceland, these sightings are rare. The number within a country border refers to the number of turtles sighted from the country indicated.

back turtle sightings during August was consistent between years (Fig. 5c).

Only 6% of 188 turtles reported by Brongersma (1972) in the North Atlantic were observed in latitudes to the north of the United Kingdom and Ireland with only one record from Iceland compared with 64 from the United Kingdom and Ireland (Fig. 6).

Discussion

For some routinely sampled groups, extensive historical databases allow range shifts over recent decades to be examined directly. For example, in the NE Atlantic, Beaugrand *et al.* (2002) used 46 777 plankton samples collected between 1958 and 1999 from the CPR survey to show northerly range shifts for many species of plankton. Similarly, in the North Sea, Perry *et al.* (2005) used samples representing 47 species of fish collected from trawl surveys between 1977 and 2001 to show northerly range shifts for a large number (21 out of 36) of species. These trends over the last couple of decades have occurred in parallel with a general warming of the NE Atlantic (Barnett *et al.*, 2001; Levitus *et al.*, 2001). However, for many species, long-term empirical datasets on distribution are lacking and yet predicting the implications of climate change is still important. It would be predicted that, for any marine species in the North Atlantic that shows a strong thermal dependence

(e.g. ectotherms such as leatherback turtles) on its distribution, that corresponding northerly shifts will also have occurred over the last couple of decades.

The leatherback turtle is the largest extant sea turtle, and maintains, among sea turtles, the most extreme thermal gradient between internal body temperature and environmental temperature (Southwood *et al.*, 2005). This ability to maintain high body temperatures minimizes the thermal barriers to habitat exploitation, allowing leatherbacks to move into high latitudes (Brongersma, 1972) and deeper waters (Bleakney, 1965; Hays *et al.*, 2004). However, despite the physiological and anatomical adaptations to heat conservation that allows regional endothermy, leatherback turtles do not commonly exploit the world's coldest oceans (Fig. 6). This suggests that there are thermal barriers, which limit the range of leatherback turtles. Although we show from the *in situ* temperature measurements that leatherback turtles experienced a wide range of temperatures (9–33 °C), the colder temperatures within this range were only experienced briefly during deep dives. Consequently, the position of the 15 °C surface isotherm effectively encapsulates the range of this species. It could be argued that because leatherback turtles have been sighted in the cold waters (<10 °C) of the North Atlantic around Norway and Iceland (Brongersma, 1972; Carriol & Vader, 2002) that our assertion that turtles are generally restricted to areas where surface water temperature is above 15 °C is flawed. However, there is a risk in interpreting the observations in this way because species that are atypical (i.e. occur infrequently and in low numbers) (e.g. leatherback turtles in the Iceland and Norway), in a region may be afforded disproportionately high research or conservation status simply because they are rare (Rodrigues & Gaston, 2002). However, viewing such sightings/occurrences in the context of the wider distribution can resolve and put into perspective such rare observations (Rodrigues & Gaston, 2002). While, we appreciate that leatherback turtles have been sighted at high latitudes, it is important to note that these events are rare and therefore probably not representative of the general behavior or distribution of leatherback turtles. Clearly, observational data are not perfect due to reporting biases, but here we use such data as simply one element of a multistranded story that suggests leatherback do not generally venture into very cold water and that the United Kingdom most probably lies near the northern limit routinely occupied by this species.

Further support for this thermal dependence of range to surface waters above 15 °C, is evident from observations of distinct seasonal peaks in leatherback occurrence centered on the time of year when surface water temperatures are warmest (above 15 °C) (i.e. in the

summer and autumn) (Brongersma, 1972). If food or prey availability were the only descriptor of the occurrence of leatherback turtles in the North Atlantic we would expect there to be a broad seasonal peak in their abundance at temperate latitudes, like that recorded for zooplankton, rather than the narrow restricted peak observed. It should be noted, however, that there is a need for datasets not only on the seasonal abundance of zooplankton but also specifically on gelatinous zooplankton upon which leatherback turtles feed. While gelatinous zooplankton have traditionally been understudied by marine ecologists, this group are now receiving more attention. For example, acoustic and aerial surveys are now being used to assess jellyfish abundance over broad spatial and temporal scales (e.g. Brierley *et al.*, 2001; Graham *et al.*, 2003) and reexamination of CPR samples may reveal the potential of this extensive dataset for mapping spatio-temporal abundance in gelatinous zooplankton.

Our conclusion that the seasonal occupation of high latitudes by leatherback turtles is primarily driven by water temperature is further supported by observations from an extensive dataset on leatherback turtle bycatch in long-line fisheries (<http://www.nmfs.noaa.gov/mediacenter/turtles/>). In this study, conducted from 2001 to 2003, a total of 1 169 864 baited hooks (164 429, 427 385 and 578 050 in 2001, 2002 and 2003, respectively) were deployed in the North East Distant (NED) reporting area of the North Atlantic, where SSTs varied between 12 and 21 °C. This study found that there was a significant relationship between the catch rate of leatherback turtles and SST, with an increase in leatherback turtle catch rates at water temperatures over 20 °C. It is possible that seasonal northerly migrations by leatherback turtles might be driven by factors aside from temperature (e.g. photoperiod) that might explain the seasonal occurrence of this species at high latitude. However, the combination of approaches we have used, certainly suggests that temperature plays a key role in determining the extent of northerly travel and the southerly retreat of individuals at the end of the summer.

We found that dive depths and dive durations differed between warmer *vs.* cooler waters and suggest two possible explanations. Firstly, the turtles diving ability is limited by temperature such that their metabolic functioning decreases at lower temperatures. However, this seems unlikely to be the sole cause for reduced dive depths and durations because leatherback turtle muscle function seems not be dependant on temperature (Penick *et al.*, 1998). Secondly, their food, which consists primarily of jellyfish (Lutcavage & Lutz, 1986; Davenport, 1998; James & Herman, 2001), is distributed differently in cold water than in warm water

so that their preferred food is found nearer the surface in cold water than in warmer water. The evidence for this is that there is more plankton, including jellyfish, in shallower waters in cold regions (Longhurst, 1995). Thus, it seems that leatherback turtle vertical distributions may be restricted by food availability, mediated by temperature.

Knowing where turtles occur is important for their conservation. For example, leatherback turtle by-catch in a range of fisheries poses a significant threat to population growth and persistence (Lewison *et al.*, 2004a, b) but can be limited by taking into account the habitat preferences of the turtles and by fishing in colder waters, i.e. $<20^{\circ}\text{C}$ or better still below 15°C . Although leatherback turtles are legally protected in UK waters and elsewhere in the Atlantic, a worrying statistic is that while 301 leatherbacks were recorded alive in the United Kingdom between 1985 and 2002, during this same period a total of 120 dead animals were also recorded. Although these relative values for alive and dead animals are probably subjected to differential reporting biases, they do highlight the need for leatherback conservation not only in the open ocean, but also in areas closer to shore.

There is now general acceptance that temperatures world wide are increasing and this warming trend is likely to continue into the foreseeable future (Stott *et al.*, 2004). This predicted temperature rise will have important implications for leatherback turtles, in that their geographical range will extend further north as the warmer waters extend into northern latitudes. Our evidence suggests that the range of leatherback turtles will have extended north by around 200 km per decade in the North East Atlantic over the last two decades. We draw attention to the inferred range expansions reported here to highlight the conservation plight of leatherback turtles. We feel that it is timely to introduce this discussion because leatherback turtles are a critically endangered species and hence it is important to describe their thermal habitats and preferences especially in the light of the predicted changes in global climate.

Acknowledgements

Satellite measured sea surface temperatures were derived from NOAA's GOES daily SST satellite data, and processed and made available at: <http://www.seaturtle.org/maptool/>. The source data have a nominal spatial resolution of 6 km and have been validated to be within 0.5°C of actual SST. To examine long-term patterns in the position of the 15°C isotherm we used AVHRR data supplied by Tim Smyth Remote Sensing Group, Plymouth Marine Laboratory as part of the NERC Remote Sensing Data Analysis Service. We wish to acknowledge use of the Maptool program for some analysis and graphics that appear in this paper. We are grateful to the Ministry of Agriculture, Forestry,

Land and Fisheries in Grenada for permission to attach transmitters to turtles on nesting beaches; Ocean Spirits Inc., Jon Houghton and Andy Myers for logistical help in the field; Moyra Hays and the late Bob Randig for help with the attachment system. We also thank Anthony Richardson for his assistance in procuring the SST data around United Kingdom, Vicky Hobson for her assistance in determining the position of the 15°C isotherm and Professors Clive Hamblen, Paul Ehrlich and Robert Paine for their insightful comments on the manuscript.

References

- Barnett TP, Pierce DW, Schnur R (2001) Detection of anthropogenic climate change in the world's oceans. *Science*, **292**, 270–274.
- Batten SD, Hirst AG, Hunter J *et al.* (1999) Mesozooplankton biomass in the Celtic Sea: a first approach to comparing and combining CPR and LHPR data. *Journal of the Marine Biological Association of the United Kingdom*, **79**, 179–181.
- Beaugrand G, Reid PC, Ibanez F *et al.* (2002) Reorganization of North Atlantic marine copepod biodiversity and climate. *Science*, **296**, 1692–1694.
- Bleakney JS (1965) Reports of marine turtles from New England and Eastern Canada. *Canadian Field-Naturalist*, **79**, 120–128.
- Brierley AS, Axelsen BE, Buecher E *et al.* (2001) Acoustic observations of jellyfish in the Namibian Benguela. *Marine Ecology Progress Series*, **210**, 55–66.
- Brongersma LD (1972) European Atlantic turtles. *Zoologische Verhandelingen (Leiden)*, **121**, 1–318.
- Carriol RP, Vader W (2002) Occurrence of *Stomatolepas elegans* (Cirripedia: Balanomorpha) on a leatherback turtle from Finnmark, northern Norway. *Journal of the Marine Biological Association of the United Kingdom*, **82**, 1033–1034.
- Caughley G, Gunn A (1996) *Conservation Biology in Theory and Practice*. Blackwell Science, Cambridge, MA.
- Davenport J (1998) Sustaining endothermy on a diet of cold jelly: energetics of the leatherback turtle *Dermochelys coriacea*. *British Herpetological Society Bulletin*, **62**, 4–8.
- Diaz H, Folland C, Manabe T *et al.* (2002) Workshop on advances in the use of historical marine climate data. *World Meteorological Organization Bulletin*, **51**, 377–380.
- Edwards M, Richardson AJ (2004) Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature*, **430**, 881–884.
- Genner MJ, Sims DW, Wearmouth VJ *et al.* (2004) Regional climatic warming drives long-term community changes of British marine fish. *Proceedings of the Royal Society of London Series B – Biological Sciences*, **271**, 655–661.
- Graham WM, Martin DL, Felder DL *et al.* (2003) Ecological and economic implications of a tropical jellyfish invader in the Gulf of Mexico. *Biological Invasions*, **5**, 53–69.
- Hays GC, Akesson S, Godley BJ *et al.* (2001) The implications of location accuracy for the interpretation of satellite-tracking data. *Animal Behaviour*, **61**, 1035–1040.
- Hays GC, Houghton JDR, Myers AE (2004) Pan-Atlantic leatherback turtle movements. *Nature*, **429**, 522.
- Hughes L (2000) Biological consequences of global warming: is the signal already apparent? *Trends in Ecology and Evolution*, **15**, 56–61.

- James MC, Herman TB (2001) Feeding of *Dermochelys coriacea* Northwest Atlantic. *Chelonian Conservation and Biology*, **4**, 202–205.
- James MC, Ottensmeyer CA, Myers RA (2005) Identification of high-use habitat and threats to leatherback sea turtles in northern waters: new directions for conservation. *Ecology Letters*, **8**, 195–201.
- Levitus S, Antonov JI, Wang J *et al.* (2001) Anthropogenic warming of earth's climate system. *Science*, **292**, 267–270.
- Lewison RL, Crowder LB, Read AJ *et al.* (2004a) Understanding impacts of fisheries bycatch on marine megafauna. *Trends in Ecology and Evolution*, **19**, 598–604.
- Lewison RL, Freeman SA, Crowder LB (2004b) Quantifying the effects of fisheries on threatened species: the impact of pelagic longlines on loggerhead and leatherback sea turtles. *Ecology Letters*, **7**, 221–231.
- Longhurst A (1995) Seasonal cycles of pelagic production and consumption. *Progress in Oceanography*, **36**, 77–167.
- Luschi P, Hays GC, Papi F (2003) A review of long-distance movements by marine turtles, and the possible role of ocean currents. *Oikos*, **103**, 293–202.
- Lutcavage M, Lutz PL (1986) Metabolic-rate and food-energy requirements of the leatherback sea-turtle, *Dermochelys coriacea*. *Copeia*, **3**, 796–798.
- McMahon CR, Autret E, Houghton JDR *et al.* (2005) Animal-borne sensors successfully capture the real-time thermal properties of ocean basins. *Limnology and Oceanography: Methods*, **3**, 392–398.
- Metcalfe JD, Arnold GP (1997) Tracking fish with electronic tags. *Nature*, **387**, 665–666.
- Orstom PR (2000) Onboard quality control of XBT bathy messages. In: *Guidelines for XBT Data* pp. 142–150. World Meteorological Organization Intergovernmental Oceanographic Commission, Paris, France.
- Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.
- Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography*, **12**, 361–371.
- Penick DN, Spotila JR, O'Connor MP *et al.* (1998) Thermal independence of muscle tissue metabolism in the leatherback turtle, *Dermochelys coriacea*. *Comparative Biochemistry and Physiology – Part A: Molecular and Integrative Physiology*, **120**, 399–403.
- Perry AL, Low PJ, Ellis JR *et al.* (2005) Climate change and distribution shifts in marine fishes. *Science*, **308**, 1912–1915.
- Pierpoint C (2000) *Bycatch of marine turtles in UK & Irish Waters*. JNCC Report No. 310, JNCC, Peterborough.
- Richardson AJ, Schoeman DS (2004) Climate impact on plankton ecosystems in the Northeast Atlantic. *Science*, **305**, 1609–1612.
- Rodrigues ASL, Gaston KJ (2002) Rarity and conservation planning across geopolitical units. *Conservation Biology*, **16**, 674–682.
- Root TL, Price JT, Hall KR *et al.* (2003) Fingerprints of global warming on wild animals and plants. *Nature*, **421**, 57–60.
- Sims DW, Southall EJ, Tarling GA *et al.* (2005) Habitat-specific normal and reverse diel vertical migration in the plankton-feeding basking shark. *Journal of Animal Ecology*, **74**, 755–761.
- Southwood AL, Andrews RD, Paladino FV *et al.* (2005) Effects of diving and swimming behavior on body temperatures of Pacific leatherback turtles in tropical seas. *Physiological and Biochemical Zoology*, **78**, 285–297.
- Stebbing ARD, Turk SMT, Wheeler A *et al.* (2002) Immigration of southern fish species to south-west England linked to warming of the North Atlantic (1960–2001). *Journal of the Marine Biological Association of the United Kingdom*, **82**, 177–180.
- Stott PA, Stone DA, Allen MR (2004) Human contribution to the European heatwave of 2003. *Nature*, **432**, 610–614.
- Warner AJ, Hays GC (1994) Sampling by the Continuous Plankton Recorder Survey. *Progress in Oceanography*, **34**, 237–256.
- White NA, Sjoberg M (2002) Accuracy of satellite positions from free-ranging grey seals using ARGOS. *Polar Biology*, **25**, 629–631.