



# Pink spot, white spot: The pineal skylight of the leatherback turtle (*Dermochelys coriacea* Vandelli 1761) skull and its possible role in the phenology of feeding migrations



John Davenport<sup>a,\*</sup>, T. Todd Jones<sup>b</sup>, Thierry M. Work<sup>c</sup>, George H. Balazs<sup>d</sup>

<sup>a</sup> School of Biological, Earth & Environmental Sciences, University College Cork, North Mall Campus Distillery Fields, Cork, Ireland

<sup>b</sup> NOAA Fisheries Service, Pacific Islands Fisheries Science Center, 1601 Kapiolani Blvd., Ste 1000, Honolulu, HI 96814, USA

<sup>c</sup> U.S. Geological Survey, National Wildlife Health Center, Honolulu Field Station, Honolulu, HI 96850, USA

<sup>d</sup> NOAA Fisheries Service, Pacific Islands Fisheries Science Center, 2570 Dole St., Honolulu, HI 96814, USA

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## ABSTRACT

Leatherback turtles, *Dermochelys coriacea*, which have an irregular pink area on the crown of the head known as the pineal or 'pink spot', forage upon jellyfish in cool temperate waters along the western and eastern margins of the North Atlantic during the summer. Our study showed that the skeletal structures underlying the pink spot in juvenile and adult turtles are compatible with the idea of a pineal dosimeter function that would support recognition of environmental light stimuli. We interrogated an extensive turtle sightings database to elucidate the phenology of leatherback foraging during summer months around Great Britain and Ireland and compared the sightings with historical data for sea surface temperatures and day lengths to assess whether sea surface temperature or light periodicity/levels were likely abiotic triggers prompting foraging turtles to turn south and leave their feeding grounds at the end of the summer. We found that sea temperature was too variable and slow changing in the study area to be useful as a trigger and suggest that shortening of day lengths as the late summer equilux is approached provides a credible phenological cue, acting via the pineal, for leatherbacks to leave their foraging areas whether they are feeding close to Nova Scotia or Great Britain and Ireland.

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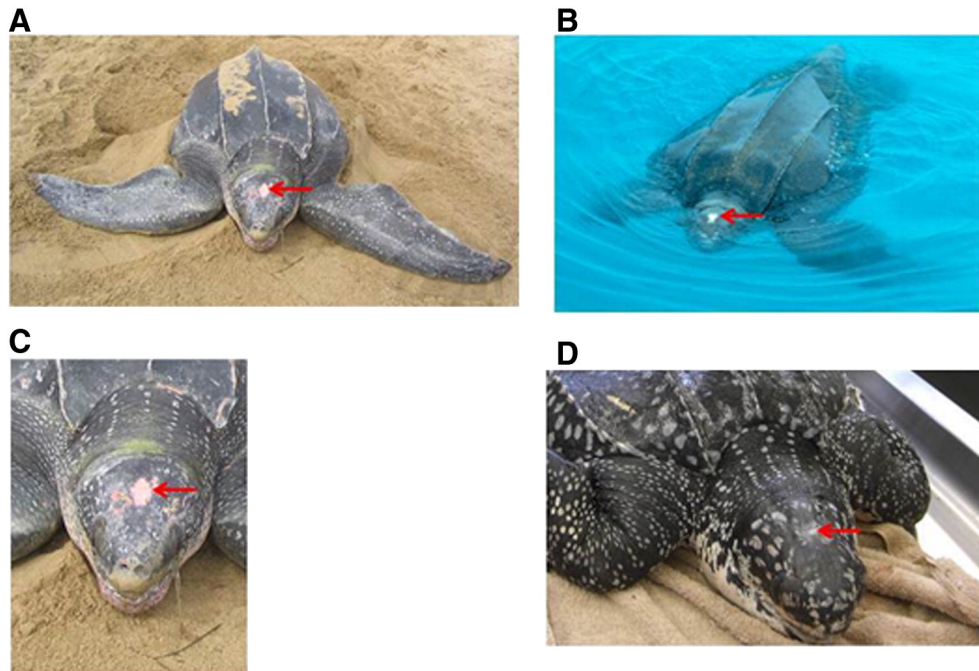
## 1. Introduction

Adult leatherback sea turtles *Dermochelys coriacea* are obligate feeders on gelatinous organisms (Davenport and Balazs, 1991; den Hartog and van Nierop, 1984). Prey densities are geographically patchy and leatherbacks migrate seasonally over long distances (as much as 18,000 km within year round trip) between breeding areas in the tropics and feeding areas in cool temperate coastal waters at higher latitudes where surface blooms of jellyfish are common (e.g., Ferraroli et al., 2004; Hays et al., 2004, 2006; James et al., 2005). These migration distances are comparable with those of birds such as waders and swallows and beyond those of similarly sized fish and marine mammals (Hays and Scott, 2013). Leatherbacks are endothermic (Bostrom et al., 2010), maintaining core temperatures of 25–27 °C when in cool temperate water (Bostrom and Jones, 2007; Casey et al., 2014; James and Mrosovsky, 2004). Furthermore, there is palaeoecological evidence that leatherbacks have foraged in cool temperate waters for more than 40 million years (Albright et al., 2003).

In the Northwest Atlantic leatherbacks forage coastally in late summer as far north as Canada (roughly 40–50°N) where September sea surface temperatures (SSTs) are 14–15 °C (James et al., 2006; Website 1). Peak numbers (1998–2005) of leatherbacks off Nova Scotia and Newfoundland occur in August; numbers decline markedly in September and October (James et al., 2006). In the Northeast Atlantic leatherbacks forage appreciably farther north, they are common around Great Britain and Ireland (roughly 50–60°N), while the northernmost record of a live leatherback was that of a turtle swimming at 71°N, 23°E (September 14, 1997) in Norwegian waters, substantially north of the Arctic Circle (Carriol and Vader, 2002). SST at this time was 10.0–10.5 °C (Website 1). McMahon and Hays (2006) investigated the TURTLE database (Penrose and Gander, 2013) and found that the peak month for leatherback turtle sightings around Great Britain and Ireland (1984–2003) was also August. In both western and eastern North Atlantic, the factors that precipitate the return of leatherbacks to waters further south as summer ends are not well known. However, McMahon and Hays (2006) also studied 9 turtles satellite-tagged in the Caribbean and equipped with SST monitors and reported that the 15 °C isotherm in the North Atlantic limited most open ocean leatherback activity, and that southerly swimming was triggered when temperatures fell to 12–18 °C.

\* Corresponding author. Tel.: +353 44 1392926233.

E-mail addresses: [j.davenport@ucc.ie](mailto:j.davenport@ucc.ie) (J. Davenport), [todd.jones@noaa.gov](mailto:todd.jones@noaa.gov) (T.T. Jones), [thierry\\_work@usgs.gov](mailto:thierry_work@usgs.gov) (T.M. Work), [gabalazs@honlab.nmfs.hawaii.edu](mailto:gabalazs@honlab.nmfs.hawaii.edu) (G.H. Balazs).



**Fig. 1.** Illustrations of pineal spots of leatherback turtles (indicated by red arrows). (A, C, close-up) Photographs of a live adult female leatherback turtle in the process of nest-covering on a beach in French Guiana (photo: Tom Doyle). Note the 'pink spot' in the centre of the parietal area. Note also that the spot has an irregular shape. (B) Photograph of a live adult leatherback turtle (sex unknown) swimming off the Isles of Scilly (approx. 50°N, 6°W) (photo: Mike Daines). Note that the pineal spot is above the water and is white. (C) Photograph of dead juvenile leatherback turtle. In this specimen, the pineal spot is small and white.

The migration of sea turtles has been extensively studied from the viewpoint of methods used to determine the directions taken by individual turtles at different stages of their life history (e.g., Lohmann and Lohmann, 1996; Lohmann et al., 2004; Papi et al., 2000; Salmon and Wyneken, 1994). However, relatively little attention has been paid to the phenology of migrations (their timing in relation to environmental stimuli). In contrast, the phenology of migration has been extensively studied in birds, in which arrival at, and departure from, breeding areas has been investigated since the 1940s and is known to be controlled primarily by photoperiod acting through the pineal body to control release of melatonin, although other factors such as climate and geographical position can provide fine control over migration dates (Cotton, 2003). Phenological migratory responses are essentially anticipatory; migration timing is designed to maximize opportunities for breeding or food capture and to avoid adverse or dangerous environmental conditions. Caprioli et al. (2012) showed that genetic control of such migration depends upon *clock* genes that occur in vertebrates from fish to birds, so are of great antiquity.

In reptiles, some groups (tuataras and several species of lizards including *Anolis* spp. and *Sceloporus* spp.) have a well-developed parietal/pineal eye, complete with retina, cornea and lens, projecting through the dorsal surface of the skull (via a parietal foramen) that acts as a radiation dosimeter (Schwab and O'Connor, 2005). No turtle has a pineal eye or a parietal foramen, but the pineal organ is well developed and situated above the tubular brain. The pineal–paraphyseal complex of cheloniid sea turtles was studied by Owens and Ralph (1978). They found that it was a large structure projecting dorsally and anteriorly above the prosencephalon of the brain. Despite the absence of a pineal eye and parietal foramen, there was histological evidence of rudimentary secretory photoreceptor cells in the pineal body, which was extensively fused with the paraphysis. Owens and Gern (1985) later confirmed secretion of melatonin by the cheloniid pineal body. Similar studies have not been carried out upon leatherback turtles, primarily because the brain is rarely recovered in good condition from dead animals (Wyneken, 2001). There is variability among sea turtles in the

closeness of the pineal to the dorsum of the skull, with that of the leatherback being closer than those of cheloniids (Wyneken, 2001).

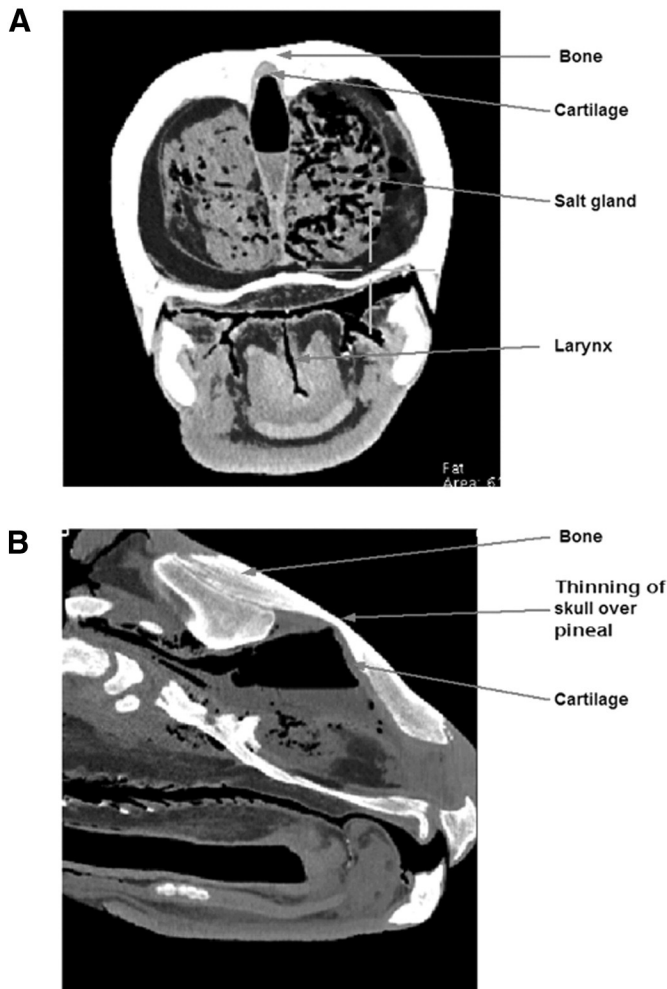
It has long been recognized that the leatherback turtle has an irregular pink area on the crown of the head (Pritchard, 1979), and this has come to be known as the pineal or 'pink spot', that can be used in photo identification of individuals (McDonald et al., 1996). Our study had two objectives. First, we investigated the skeletal structures underlying the pink spot in juvenile and adult turtles to determine whether they are compatible with a dosimeter function that would support recognition of environmental light stimuli. Second, we interrogated an extensive turtle sightings database (TURTLE vs 1.2; Penrose and Gander, 2013) to elucidate the phenology of leatherback foraging around Great Britain and Ireland, and to assess whether light periodicity or levels were likely triggers for foraging turtles to turn south and leave their feeding grounds at the end of the summer.

## 2. Methods

### 2.1. Collection and autopsy of turtles

Three juvenile leatherbacks (66.7–83.0 cm straight carapace length [SCL], 33.2–53.5 kg body mass) were collected as bycatch by observers (NOAA Fisheries, Pacific Islands Regional Office, Observer Program) on long-line fishing vessels operating in the equatorial Pacific. Frozen immediately after death, they were in good post-mortem condition. Turtles were thawed 24 h before necropsy, which entailed a complete external and internal examination with procurement of tissues for routine histopathology to confirm cause of death (drowning) (cf. Work and Balazs, 2002, 2010). This involved gross dissection of the head during which transmissibility of the pineal region to light was investigated. The skulls of two of the juveniles (74.1 and 83.0 cm SCL) were X-rayed post-dissection.

An adult leatherback studied was found dead close to the shore at Ballycotton, East Cork, Ireland, on 24 July 2007. The female was 168 cm in curved carapace length, so it would probably have weighed



**Fig. 2.** (A) Transverse CT scan of the head of an adult female leatherback turtle at the level of the pineal organ (skull width: 179 mm). (B) Sagittal CT scan of the same turtle head (height at the level of the pineal: 228 mm). The area of the parietal bones overlaying the pineal is much thinner than the general dorsal skull bones.

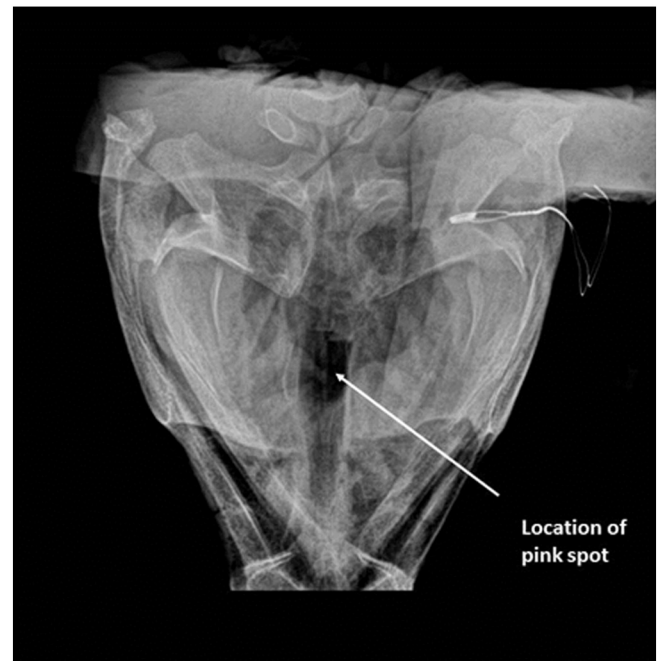
around 450 kg (cf. Georges and Fossette, 2006). The head and neck were removed (amputated as close as possible to the body) and transferred to a freezer; the remainder of the carcass was disposed of at sea. The head and neck were later embalmed in the Department of Anatomy, University College Cork (for details, see Davenport et al., 2009) before CT scanning and dissection. After soft-tissue study, the skull was prepared for museum display and its transmissibility to light investigated.

## 2.2. Digital imaging

The head and neck of the adult turtle were CT scanned (1 mm slice acquisition with a bony reconstruction algorithm) using a Siemens Somatom Plus 4 scanner (Erlangen, Germany). Sagittal and transverse sections of the CT reconstruction were inspected to determine the skull structure in the pineal region. The heads of two of the juvenile leatherbacks were imaged with a Vet Ray Technology digital X-ray system by Sedecal (Sedecal USA, 230 Lexington Drive, Buffalo Grove, Illinois USA) at the Makai Animal Clinic (Kailua, Hawaii USA). The heads were imaged along the dorsoventral axis.

## 2.3. Turtle sightings and environmental data

Leatherback turtle sightings around Great Britain and Ireland were analyzed using information held on the TURTLE database (Penrose and Gander, 2013). This database contains historical sightings data for



**Fig. 3.** X-radiograph of the skull of a juvenile leatherback turtle (from above; Skull maximum width 120 mm; skull length 156 mm). Note the radio-transparent area in the region of the 'pink spot'.

leatherbacks from 1756 to the present and is added to by a reporting network that has functioned in a standard fashion since 2001 but has been effective since the late 1980s. First, the 2002–2012 data set was examined and filtered, so that only leatherbacks that had been sighted alive at sea, and for which the sighting date could be firmly established, were analyzed. Thus, unidentified species, stranded (live or dead) turtles and leatherbacks for which sighting date was uncertain were excluded. This left 369 sighting records, reflecting seasonal patterns of sightings over a recent decade. Sighting dates were converted to day-of-year values (taking account of leap years) prior to statistical analysis. Next, the 1989–2012 data set was inspected to determine the first and last sighting dates of a given year ( $n = 24$  in each case).

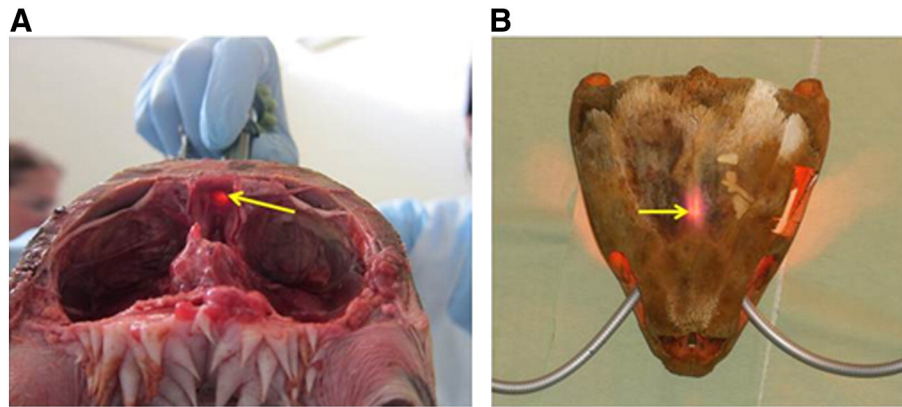
Two other data sets were interrogated for comparison with the sightings data. First, monthly mean optimum interpolation SSTs (1961–1990) were collected from the northernmost part of Great Britain (60°N; Shetland) and the southernmost part (50°N, Isles of Scilly) (Website 1). Second, day length data for 50°N (off Isles of Scilly) and 60°N (off Shetland) in 2012 were obtained (Website 2).

## 3. Results

### 3.1. Anatomical findings

Fig. 1 illustrates the pineal spot of adult and juvenile leatherback turtles. The photographs of the adult female nest-covering in French Guiana (Fig. 1A, C) show the expected melanin-deficient pink areas of the skin over the parietal area. In contrast, the adult swimming close to the Isles of Scilly, UK (in water no warmer than 16 °C; see Fig. 5A), with its head out of water had a white pineal spot (Fig. 1B), as does the dead juvenile leatherback shown in Fig. 1D. We interpret these images as indicating that the pink colour of the pineal spot in nesting leatherbacks reflects strong subcutaneous blood flow during the exertion of the beach crawl and nest digging/covering. Circulation is absent in the dead juvenile, while the adult turtle swimming in cool water off the Isles of Scilly was likely employing peripheral vasoconstriction to limit heat loss. We note that the pineal spot always appears white in underwater photographs of leatherback turtles taken in cool or warm waters; this would be the case whether the spot was actually pink or white





**Fig. 4.** (A) Photograph of the roof of the skull of a juvenile leatherback turtle in which the skull has been sawn transversely posterior to the eyes and the salt glands removed. A small torch (delivering white light) is being held against the dorsal surface of the parietal area. Light (predominantly red; indicated by yellow arrow) can be seen shining through the skin and parietal. (B) Dorsal photograph of skull of adult female leatherback with two white light sources placed within the skull. Note the central red light spot (indicated by yellow arrow) shining through the medial junction of the parietal bones. The bone window cut in the left postorbital/squamosal bones was created for another study (Davenport et al., 2009).

because red light is substantially absorbed within a few centimeters of water path.

Fig. 2, derived from CT scanning, shows that the neurocranial cavity in the pineal region is covered dorsally by thin layers of bone and cartilage (~2.6 mm and 3.5 mm thick, respectively). In transverse section (Fig. 2A), it is evident that there is a pronounced narrow (13.6 mm) cavity in the skull dorsum, partly filled with cartilage, projecting dorsally out of the neurocranial cavity; this has been shown previously by Wyneken (2001). The skull that it penetrates is about 24 mm thick at this point. Fig. 2B shows that this cavity is much longer antero-posteriorly than transversely. In particular, the medial thinning of the parietal bone is about 46 mm long. Fig. 3 reveals the shape of the thin area of the parietal bones more clearly. This X-radiograph of the head of a juvenile turtle (skull width 120 mm; skull length 156 mm) shows that the area has an oblong shape, the length being about 1.7 × breadth.

Fig. 4A establishes that light readily passes through the roof of the skull in the pineal region of juvenile leatherback turtles; it also indicates that red light is preferentially transmitted. Fig. 4B confirms that this is true of adult leatherbacks too, and that the thin area of the skull is oblong in shape. Effectively, the leatherback skull has a dorsal radiation-transparent area ('skylight') that allows ambient light to bathe the pineal organ.

### 3.2. Analysis of sightings data for Great Britain and Ireland

Surface temperature data (averaged over a 30-year period; Fig. 5A) indicate that there are substantial surface temperature differences (2–5 °C) between the northern and southern limits of the coastal feeding area. It is also evident that rates of change in temperature in late summer/early autumn are low. These are long-term averages, and inter-annual variation is great because of variations in weather patterns; temperatures also tend to be more variable close to coasts. Overall, these data indicate that, within the broad range of temperatures tolerated by leatherbacks, a specific SST is unlikely to provide a reliable signal for a leatherback foraging off Great Britain and Ireland to cease feeding and turn south.

Day length data (Fig. 5B) also show differences between 50°N and 60°N (summer day length being greater at higher latitude), but they also reveal an interesting feature that is virtually independent of latitude between 40 and 70°N; the timing of equality of length of day and night (equinox, which is close to, but not identical to the equinox), i.e., when both are 12 h long. At a longitude of 5°W, this timing in late summer equates to 25–26 September at 40°N and 24–25 September at 70°N (about days of year = 267–269).

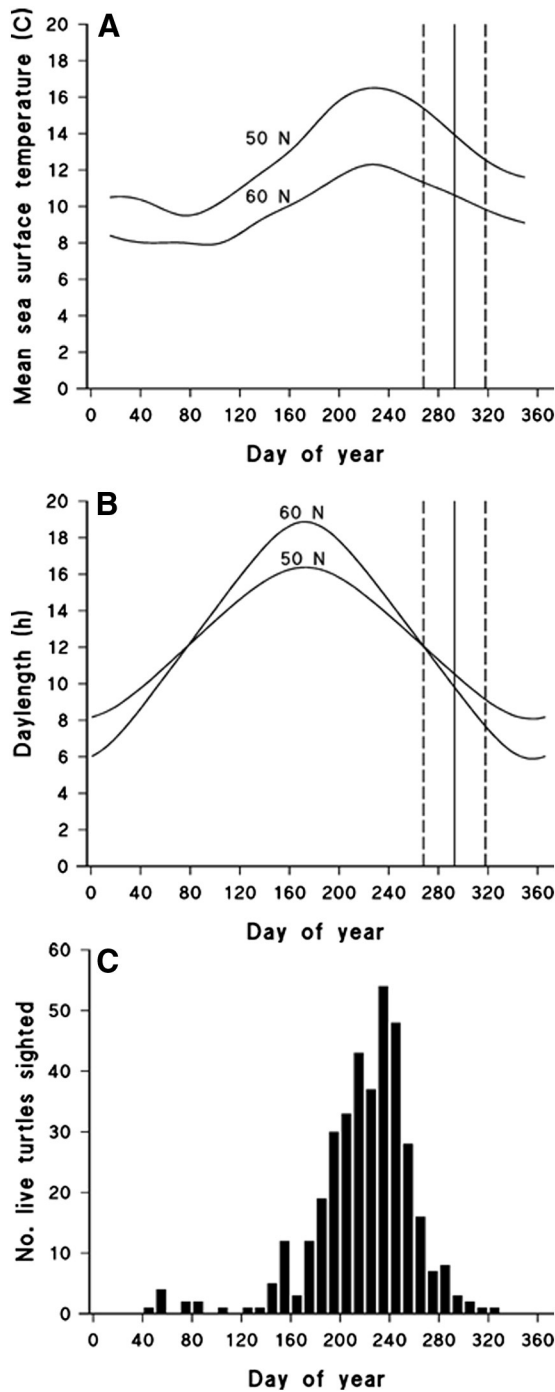
Leatherback sightings for 2002–2012 around Great Britain and Ireland are displayed in Fig. 5C. Their distribution is non-normal

(Anderson–Darling;  $p < 0.0005$ ) and skewed towards late summer. The median sighting date corresponds to August 14–15. Inspection of the 1989–2012 data set revealed that leatherback sightings have been reported from every month of the year, although sightings in winter are sporadic and rare. Mean first sighting date (1989–2012,  $n = 24$ ) was June 3 (days of year = 154, SD = 58); mean last sighting date was October 20 (days of year = 293, SD = 25). Last sightings data were normally distributed (Anderson–Darling;  $p = 0.716$ ), while first sightings were not (Anderson–Darling;  $p = 0.004$ ). The autumn equinox occurs within one standard deviation of the mean last sighting date (Fig. 4B). The 2002–2012 data set was also searched for winter (December–February inclusive) sightings ( $n = 5$ ) of live leatherbacks at sea. These were correlated with contemporaneous SSTs (Table 1), which ranged from 8.5 °C to 11.0 °C.

## 4. Discussion

North Atlantic leatherback turtles could be compelled to leave their northern feeding grounds in late summer/early autumn for multiple reasons. First, at this time of year, the local abundance of the large gelatinous prey that attract them to northern coastal foraging grounds (e.g., *Cyanea capillata*, *Rhizostoma octopus* and *Aurelia aurita*) tends to diminish, making foraging less efficient. It should be noted that this is not true of oceanic waters (where leatherbacks spend most of their time) as many medusa, salps and pyrosomas have a year-round presence, especially at depth (Houghton et al., 2008). Second, water temperatures are likely to decline, making maintenance of a high body temperature energetically more expensive (Paladino et al., 1990). By turning south in September/October, leatherbacks will largely avoid these adverse conditions.

The jellyfish prey of leatherback turtles are patchy both temporally and geographically within years around Great Britain and Ireland, and the densities of medusae vary stochastically from year to year (Houghton et al., 2006, 2007; Doyle et al., 2007). It is therefore unlikely that a low food density alone provides a reliable biotic signal to cause leatherbacks to swim south from their late summer feeding grounds. Abiotic signals such as temperature or photoperiod are potentially more reliable, although both are modified by weather, so responses to them will likely vary from year to year. The data presented here suggest that surface water temperature is probably less important than photoperiod in triggering the southern migration, at least in relatively shallow, coastal waters around Great Britain and Ireland, where temperatures are much more variable than in the open ocean. It is noteworthy that the most northerly record of a live, swimming leatherback turtle occurred before the autumn equinox (Carriol and Vader, 2002), when the surface temperature was 10.0–10.5 °C. We note also that a



**Fig. 5.** Relationships between sea surface temperatures, day length and timing of leatherback turtle sightings around Great Britain and Ireland. (A) Mean monthly sea surface temperatures (1961–1990) at 50°N (off the Isles of Scilly) and 60°N (off Shetland). (B) Day length at 50°N (off Scilly Isles) and 60°N (off Shetland) in 2012. (C) Records of sightings of live leatherback turtles at sea around Great Britain and Ireland (2002–2012;  $n = 369$ ). Data are presented in 10-day duration bins. Solid vertical line indicates mean last live leatherback sighting date of the year (1989–2012;  $n = 24$ ), dashed lines indicate  $\pm 1$  SD.

small proportion of coastal leatherbacks apparently overwinter at low surface temperatures (8.5–11.0 °C). Whether these are doomed turtles, or simply indicate that *D. coriacea* is a 'partial migrator', as is the case for some birds (e.g., Chan, 2001), is currently unknown, but it is evident that the 15 °C isotherm is not an absolute northern barrier to near-shore foragers. Davenport et al. (2011) showed that foraging

**Table 1**

Dates, sites and sea surface temperatures (Website 1, nearest 0.5 °C) for live leatherback turtles observed in winter (December–February) at sea around Great Britain and Ireland, 2002–2012.

Date	Site (nearest land)	Latitude/longitude	SST
01-01-2004	Cape Clear, Ireland	51°25'N, 9°31'W	10.5 °C
20-02-2004	Mevagissey, England	50°16'N, 4°31'W	10.0 °C
25-02-2005	Falmouth, England	50°03'N, 5°19'W	9.5 °C
15-11-2007	Blaskets, Ireland	52°03'N, 10°40'W	11.0 °C
16-11-2008	Granton Harbour, Scotland	55°59'N, 3°13'W	8.5 °C

leatherbacks in Canadian waters put on considerable amounts of extra insulating blubber during the foraging season. It seems probable that leatherbacks' resistance to low temperature also increases, permitting further penetration north (as well as possible overwintering).

Meissl and Ueckl (1980) studied pineal sensitivity to light in the chelonian *Trachemys scripta elegans*, the red-eared slider. They showed that the turtle's pineal was extremely sensitive to light, which had an inhibitory effect on cellular electrical activity and hence melatonin secretion. They also showed that tissues between the pineal and the environment (skin, skull, meninges and blood vessels) profoundly reduced the light levels reaching the anterior part of the pineal and selectively favored the transmission of longer (more red) wavelengths. They concluded that light would only reach the pineals of intact sliders under scotopic (well-lit) conditions; this contrasted with some fish and amphibians whose pineals responded under scotopic (dim-lit) conditions. We suggest that, in leatherback turtles, the thin parietal bones in the pineal region, the absence of melanin over the pineal spot and the ability to control cutaneous blood flow in the parietal region all contribute to enhance pineal sensitivity to light, which has a lower intensity at higher latitudes in summer. These factors are not seen in cheloniid turtles, which do not feed at such high latitudes.

If a leatherback's turn south was triggered by the autumn equinox (September 24–26), it could begin when the turtle was in the northern or southerly parts of its feeding grounds off Europe or Canada. Thus, most turtles will still be observable in the feeding grounds after they have begun their turn south and the last sighting date will be later than the average date of departure for the southern migration. In British and Irish waters, a small number of leatherbacks that appear not to leave as there are occasional reports of turtles from December and January, including sightings of these animals, will make the mean last sighting date even later than the mean date of departure. In British waters, the mean last sighting date was October 20, some 24–26 days later than the equinox. Timing of the equinox can be affected by local weather conditions. Clear, bright weather will tend to increase effective day length, while overcast weather will decrease it. The period of residence in the feeding area after turning south can be substantial. The area of leatherback feeding grounds around Great Britain and Ireland in which the turtles are likely to be observed at sea, or from land, is some 1100–1200 km from north to south. Casey et al. (2014) reported that feeding leatherbacks travelled at about 1.5 km h<sup>-1</sup> but accelerated to 2.7 km h<sup>-1</sup> when leaving the feeding grounds, so they are capable of covering 1200 km in about 18 days, assuming that they swim at this speed continually.

Overall, we suggest that day lengths close to those of the late summer equinox provide a credible phenological cue, acting via the pineal, for leatherbacks to leave their foraging areas. However, we recognize that the pineal response is likely to be part of a hierarchy of environmental and endogenous responses. The basic 15 °C isotherm 'swim south' response exhibited by oceanic turtles (McMahon and Hays, 2006) will tend to keep them out of too-cold water, whatever the time of the year (i.e., it is not a phenological response *per se*). In coastal waters, it is likely that a mix of food availability, fat reserves and photoperiod are more effective than straightforward temperature cues.

## Authors' contributions

The work presented here was carried out in close collaboration between all authors. JD wrote the first draft of the paper and the final revision; all other authors contributed to refining and finalizing the manuscript.

## Disclosure statement

We wish to confirm that there are no known conflicts of interest associated with this publication and that there has been no financial support for this work that could have influenced its outcome. The manuscript has been read and approved by all named authors.

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