During the past century, the average global temperature has increased by 0.6°K with a corresponding rise in the amount of carbon and heat stored in the world's oceans (Falkowski et al. 1998; Levitus et al. 2000, 2001). Changes in the amount of carbon and energy stored and transported around the world's oceans are critical components in understanding and forecasting changes in the earth's climate (Falkowski et al. 1998; Levitus et al. 2000, 2001) because oceans are the "flywheel" of the global climate system. Indeed, the oceans and climate are so inextricably linked that climate change may be directly related to how vigorously ocean currents transport heat from low to high latitudes (McManus et al. 2004; Sarmiento et al. 2004). The significance of the ocean is that it stores a much greater quantity of energy than the atmosphere, in essence acting as the earth's heat repository. Generally the world's oceans can be divided into two distinct layers, which differ in the scale of their interaction with the overlying atmosphere. The lower layer comprises the cold deep-water sphere, making up 80% of the oceans volume. The upper layer, which has closest contact with the atmosphere, is the seasonal boundary layer that extends down to a depth of 100 m in the tropics and several kilometers in polar regions. It is the seasonal boundary layer that is an important component of climate change, because it is in this layer that much, 30 times more than in the atmosphere, of the earth's heat is stored (Henderson-Sellers and Robinson 1986). Thus, for any given change in heat content of the ocean-atmosphere system, the temperature change in...
the atmosphere will be 30 times greater than that in the ocean. Clearly, small changes to the energy content of the oceans could have considerable effects on global climate and detecting these small changes undoubtedly requires that ocean temperatures be measured accurately and with high precision. Indeed, recognition and an increasing appreciation of the dominant role that the world’s oceans play in climate regulation (e.g., Alexander et al. 2002; Gregg et al. 2003; Sutton and Allen 1997) has led to the need for increasingly fine-scale oceanographic information. So great is the requirement for detailed climate information that the demand by far outweighs the availability, because of, amongst other reasons, the high cost of the instrumentation required to collect oceanographic information and the relatively sparse coverage by monitoring devices in the world’s oceans (Anonymous 2001).

One solution to resolving this paucity of data is to use the fine-scale oceanographic information that is collected when investigating the distribution and pelagic behavior of marine animals (Hooker and Boyd 2003; Lydersen et al. 2004, 2002). The concept of using animals as oceanographic platforms is not new (Boehlert et al. 2001; Weimerskirch et al. 1995), but has only recently become feasible because the technological tools to produce effective monitoring equipment have only recently been developed. These include small, low power microelectronics and computing techniques (Fedak 2004; Fedak et al. 2002; Kooyman 2004). These refinements have created a synergism between the biological studies of marine vertebrates and oceanographic studies (Lydersen et al. 2004) that allow us to explore the links between animal behavior, foraging activity, and oceanographic features, such as frontal systems, local eddies, and thermoclines in real time while the animals are still at sea. It follows that larger marine species in particular (because they are able to carry larger devices) may be used as platforms of opportunity to gather detailed oceanographic information especially, because these animals can collect information from logistically difficult areas, at fine temporal and spatial resolution, and at relatively low cost (Lydersen et al. 2004).

Validation of the quality of environmental data collected by “animal oceanographers” is central to this emerging area of ocean monitoring. Some previous work using data loggers deployed on animals that were subsequently recaptured to allow logger removal has addressed this issue of the data reliability (e.g., Boehlert et al. 2001). This approach of using data loggers can only be used with certain animals because of the necessity for recapture, but has the advantage that data loggers can record environmental data at high frequency and then be recalibrated when they are recovered. Relaying environmental data remotely from free-ranging animals that are not recaptured has potentially greater utility in that a wider set of species can be used. However, there are two key obstacles that need to be overcome with this approach. First there is limited bandwidth available within the most widely used satellite system, Service Argos (http://www.cls.fr/manual/default.htm), so that elegant data compression tactics are needed to recover large amounts of data. Second, if sensors are not recovered, they cannot be recalibrated and hence require long-term stability. Here we tackle these two issues and show that high quality temperature data can be relayed via satellite over long periods from broadly ranging animals.

Materials and procedures

During May to July 2003 seven free-living leatherback turtles (*Dermochelys coriacea*) were equipped with state-of-the-art Satellite Relay Data Loggers (SRDLs) to study their behavior and to demonstrate the utility of ocean temperature measurements made in this fashion (see Hays et al. [2004] for attachment protocols). In addition to the primary function of gathering data about turtle behavior, the SRDLs were programmed to measure temperature upcasts on the deepest dive in each 12-h period (provided that the dive reached a depth of at least 25 m). To measure temperature, the SRDL contains a bead-in-glass thermoprobe (G.E. Thermometrics) mounted in the water flow at the front of the speed sensor. These devices are aged by baking at 300°C to accelerate the drift that is inherent in silicon thermistors. Each device is then calibrated at 0°C, 10°C, and 25°C to produce coefficients of the Steinhart-Hart relationship between log (resistance) and temperature (Steinhart and Hart 1968). To ensure that the resistance of the thermistor is faithfully captured by the SRDL before being converted to temperature, a further calibration is performed which uses fixed precision resistors to identify and remove the effect of component variations in each SRDL’s analogue measurement circuitry. The manufacturer’s stated time constant for the thermoprobe (plunge into still water) is 300 ms.

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 5-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 ARGOS message. The resulting data string was stored in a buffer where it was made available for transmission for up to 5 d. 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 excluded data for one of the seven SRDLs because we identified a software error, which resulted in an uplink error when the SRDL transmitted information to ARGOS. Because sampling effects coupled with a change in measurement range were possible in our data set, we restricted the validation to those times (for each of the SRDLs) when a wide range of temperatures was being recorded.
To validate the temperatures recorded by the SRDLs, we compared these SRDL temperatures to those measured by the network of ARGO floats deployed in the North Atlantic Ocean (http://www.ifremer.fr/coriolis/cdc/default.htm). The temperature and pressure sensors of ARGO floats are considered stable (Oka and Ando 2004). The ARGO floats drift freely at a predetermined parking pressure (typically 2000 dbar) and make an ascent to the sea surface at a predetermined interval (every 10 d). During the ascent, they measure temperature, conductivity, and pressure with a conductivity-temperature-depth (CTD) sensor module. While staying at the sea surface, they transmit the onboard processed temperature and computed salinity data to ARGOS satellites, a process which also permits their location to be derived. These data are then passed through an automatic quality control procedure before incorporation in the final global data set. Specifically, the ARGO data-set we used consisted of mean temperatures for weekly intervals for individual pixels covering 0.32° latitude by 0.33° longitude, with mean temperature calculated for the following depths: 20 m, 50 m, 100 m, 160 m, 200 m, 300 m, 400 m, and 500 m. For each SRDL profile, the temperature at 20 m, 50 m, 100 m, 160 m, 200 m, 300 m, 400 m, 100 m, and 500 m was determined by interpolation (from the temperature-depth cast measured by the SRDL) and then compared to the mean temperatures for that pixel at corresponding depth obtained from the ARGO data-set. Our aim here is not to show that the SRDL and ARGO temperature data are perfect copies of one another as this is an unrealistic expectation given that: (1) the ARGO and SRDL data are not recorded at exactly the same locations and (2) the oceans are not homogenous. Therefore we expect there to be some differences in the records because of the occurrence of mesoscale features such as rings, eddies, etc. that are common to all ocean basins. So differences between individual SRDL and ARGO point comparison are predicted, and our aim is to determine whether the SRDL temperature data on average mimic the ARGO temperature data.

**Assessment**

The six leatherback turtles equipped with SRDLs were at sea for a total of 1284 days during which time a maximum of 2568 depth-temperature profiles could have been collected. We received depth-temperature profiles for 1560 individual dives, i.e., 61% of the potential transmittable dives. The mean maximum dive depth was 57 m (Fig. 1a). Most dives (99.5%) were shallower than 350 m (Fig. 1b). The depth-temperature profiles obtained from the SRDLs were typical of the vertical temperature stratification recorded across the North Atlantic from concurrent \( n = 379 \) profiles independently recorded by the ARGO float network (Fig. 2a). We could find no evidence for any systematic bias or drift in the SRDL data (Fig. 2b). Specifically we found that (1) the mean residual (difference between SRDL and ARGO recorded temperatures) over time for each of the six SRDLs did not differ from zero \( (P = 0.05 \text{ for each of the paired } t \text{ tests}) \) and (2) there was no systematic drift in thermistor performance (Fig. 2b). We therefore conclude that the animal-borne thermistors faithfully recorded ocean temperatures at depths between 20 m and 400 m for over 300 d while the turtles were at sea and ranging across a wide area of the Atlantic Ocean (Fig. 2). We were therefore confident that variations in our temperature observations were bona fide (Figs. 3 and 4) and that the temperature profiles recorded by the turtle SRDLs can provide a means for observing and studying oceanic features and animal behavior at or across features such as the Gulf Stream (Fig. 3) as the animals move between different regions and water bodies within ocean basins over long periods of time (Fig. 4).

**Discussion**

Service Argos is currently tracking around 1000 marine animals, this number having increased from around 200 animals in 1995 (Breonce pers. comm. unref.). Many of these animals will be carrying devices with the capacity to record and transmit environmental parameters such as water temperature. It is vital that these vast datasets are subjected to rigorous quality
control before application and also during deployment. Here we confirm that the animal-borne devices used in this study can reliably make measurements over huge spatial scales, over long time periods and over biogeochemically important ocean depths. Crucially the measurements that were made maintained their consistency over time, suggesting that sensor drift on such long deployments does not impact the value of the measurements. This finding is important given the ongoing widespread deployment of SRDLs to record water temperature, for example within the Tagging of Pacific Pelagics project which forms part of the Census for Marine Life program (Block 2005). We show the value of temperature data provided by such programs. It is, however, important to stress that device quality is not uniform and although the SRDLs used in this study have proved to be highly reliable, the same assumption cannot be made, without validation, of other types of instrument.

The incorporation of oceanographic quality sensors into animal-borne recording instruments (Fedak 2004) and now the validation of these data removes two of the major obstacles in incorporating data collected by marine animals into oceanographic and climate models and, therefore, using marine animals as oceanographers. These important advances have not removed all the limitations of using marine animals as complimentary oceanographers: one criticism is that the animal samplers do not sample randomly; nor do they follow pre-set transect coverage like those from ships. We and others

Fig. 2. Movements of six female leatherback turtles equipped with high quality thermistors that recorded ocean temperature up to depths of 1100 m showing (a) that the ocean temperatures measured by the turtle-borne thermistors faithfully represented ocean temperature ($y = 0.9883x + 0.1559$, $r^2 = 0.9602$), that the intercept did not differ from zero (95% confidence intervals: −0.2964 to 0.608), and that the fitted line did not differ from the line of equivalence (95% confidence intervals: 0.968 to 1.01) and (b) that there was no drift in the thermistor performance. The underlying sea surface temperature (SST) plot is a general representation of the SSTs at the start of the boreal summer (day of the year 130) in the North Atlantic to show the range of temperatures that turtles might encounter in this ocean basin.
(Brierley et al. 2002; Hooker and Boyd 2003) do not view this as an obstacle because animals that faithfully follow routes to and from foraging zones and are loyal to foraging areas provide a unique opportunity to observe and study site-specific longitudinal trends in key environmental parameters such as temperature. Such trends are important in detecting and quantifying long-term changes in ocean features, ocean structure, and global climate change (Fukasawa et al. 2004). However, the point still remains that animal oceanographers do not sample the ocean randomly and that parts of ocean basins may remain under-sampled. With our validation of data relayed via satellite from animal-borne platforms, we show that sampling devices no longer need to be recovered, as was the case historically with data loggers. Hence devices can now be deployed on many more species thus increasing the areas sampled in the world’s oceans.

**Comments and recommendations**

We appreciate that ocean-temperature data recorded by marine vertebrates are unlikely to replace oceanographic data collected via shipboard surveys and fixed ocean buoys. Nonetheless, it is highly probable that given the accuracy and long-term precision, as shown here, of these data that much of this information—some of which is unique in that it is collected from remote inaccessible locations (e.g., Charrassin et al. 2002)—can be incorporated into global oceanographic data sets. Indeed, incorporating remotely sensed data, such as those discussed herein, is an important step in making the data...
available to the wider scientific community so that the information can be used not only for biological studies but also oceanographic studies requiring information from remote locations. A precedent for the inclusion of oceanographic information gathered by animal oceanographers in publicly accessible databases has been set (Boehlert et al. 2001; Guinet 2005) and what remains is that the scientific community using animals as oceanographers be encouraged to make available their data to large accessible data bases such as ARGO. Inclusion of these data from marine animals sensors will therefore play an increasingly important role not only in the study of animal behavior but also in the study of global climate change.

**Fig. 4.** The migration track of a turtle showing the decrease in ocean temperature as she traveled north from her breeding grounds in the Caribbean and showing the consistency of the temperature measurements within different thermal zones (A, B, C, and D). The warmest ocean temperatures were recorded in the tropics during April and May 2003 soon after the SRDL was deployed, but these temperatures decreased as the animal moved north into more temperate waters. It is interesting to note here that the turtle started to migrate south once the water temperature dropped to approximately 15°C. The underlying SST plot is a general representation of the SSTs at the start of the boreal summer (day 130) in the North Atlantic to show the range of temperatures and the general cooling of the ocean as the turtle migrated north. The symbols on the map show the locations of the temperature profiles shown in the inset.
References


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