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Tools for studying animal behaviour: validation of dive profiles relayed via the Argos satellite system

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Central to many behavioural and ecological studies is the need to record the movements and performance of free-living animals. The challenge of making such measurements is particularly acute in marine settings where animals are often submerged and/or far from shore, making direct observations difficult. Consequently, animal-borne electronic devices now play a crucial role in studies of marine vertebrates. However, there is currently a marked dichotomy in the types of behavioural data that can be collected using these devices.

On the one hand, data loggers have expanded massively in memory and the range of parameters they can measure. For example, data are now routinely being collected on depth (Laidre et al. 2003), water temperature (Metcalfe & Arnold 1997), animal swim speed, acceleration/flipper beat frequency (Williams et al. 2000; Wilson et al. 2002) and compass heading (Davis et al. 2003). Furthermore, a range of logging visual-imaging systems provide a view of an animal's behaviour in relation to its immediate environment (e.g. Takahashi et al. 2004; Reina et al. 2005). A key limitation of these archival devices is that they must be recovered in order to obtain data. This makes them suitable for studies on species that will return to predictable locations (e.g. during the breeding season, seals and penguins return to provision offspring) or if used in conjunction with other devices to facilitate recovery (e.g. pop-off systems and VHF transmitters).

On the other hand, to obtain information from animals that move large distances and where instrument recovery is not possible, the standard technique is to use the Argos satellite system (http://www.argosinc.com). Behavioural data relayed remotely via the Argos satellite system are constrained by the limited bandwidth available, with transmissions (uplinks) limited to 256 bits of data and a typical interval of 40–200 s between transmissions depending on the application. To put these values into a more accessible context, if a single depth value was sent as an 8-bit number, only 32 depth values could be sent in a single uplink, even without any information on the timing of each depth reading. However, typically depth will be recorded every few seconds to examine dive profiles, so that in a single day many thousands of depth values will be recorded. Furthermore, many marine vertebrates spend most of their time submerged, further limiting the time available for communication with satellites. The problem readily becomes apparent: devices can record data at a much faster rate than can be relayed via the Argos system. For many years this limited bandwidth has meant that even routinely collected data on temperature, depth and dive duration have had to be grouped into bins prior to transmission or simply averaged (Hughes et al. 1998). To circumvent the limited bandwidth of Argos, novel compression techniques for relaying both temperature and depth data have been developed to allow reconstruction of temperature and depth profiles (Fedak et al. 2002). We attempted to validate this approach by simultaneously deploying two instruments on to a deep-diving marine animal, the leatherback turtle, *Dermochelys coriacea*: a satellite tag incorporating these on-board compression techniques along with a traditional time–depth recorder (TDR).

Methods

We obtained synchronous dive records from an adult female leatherback turtle with a DST-Milli (Star-Oddi, Reykjavik, Iceland) Time Depth Recorder (TDR) and a Series 9000 Satellite Relayed Data Logger (SRDL) (Sea Mammal Research Unit, St Andrews, U.K., unit cost circa £3200). The DST-Milli TDR (12.5 × 38.4 mm, 9.2 g in air, 5 g in water) had a memory capacity that allowed 21 738 depth readings with an accuracy of 0.27 m. We used a sampling interval of 1 min, to obtain data for 15 days. In

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a separate study this device successfully recorded depths of over 500 m. We used only dives longer than 6 min, to ensure a minimum of five TDR depth readings. Given the 1-min sampling interval, we assumed that dives started, on average, 30 s before the first reading deeper than 10 m and ended 30 s after the last reading deeper than 10 m.

The SRDL included a pressure sensor, which measured the depth to an accuracy of 0.33 m every 4 s. These depth values were analysed by bespoke software on board the SRDL before transmission via the Argos system. Individual dives were recorded when the depth exceeded 10 m. The start of these dives was defined by the time that the saltwater switch on the SRDL perceived that the transmitter was submerged, and the end of the dive was defined when either the saltwater switch recorded the transmitter breaking the surface, or the depth became less than 2 m. Once a dive was completed, onboard software examined the dive profile and determined the time and depth of the five most marked points of inflection during the dive (Fedak et al. 2002). The time and depth of these five points, along with the time of the end of the dive and dive duration, were then transmitted. This onboard data reduction meant that a large number of dive profiles could be obtained despite the limited bandwidth of the Argos satellite system (256 bits transmitted every 40–200 s). Typically the SRDL relayed two dive profiles in a single Argos message. In practice, individual dive profiles are supplemented with summary data on dive performance in a user-set interval, swim speed and water temperature data, and diagnostic data showing transmitter performance. Each dive entered a buffer within the SRDL so that these data would be randomly transmitted for the next 5 days. In this way, the specific dive profiles obtained via the Argos system were not weighted by the surfacing behaviour of the turtle immediately subsequent to each dive. Each dive profile transmitted by the SRDL was assigned a 'residual value' indicating how accurately the profile reconstructed from the transmitted points of inflection reflected the 'true' dive profile recorded from the original depth values measured every 4 s. The residual value is the average deviation from the original depth values to the reconstructed profile (measured in metres). Lower residual values therefore indicate greater confidence in the accuracy of the reconstructed dive profile. This calculation of residual values was performed onboard the SRDL prior to transmission of dive data. The SRDL used in this study was simply randomly selected from a number of available units and had identical hardware and software configurations to other SRDL units that are being widely used in marine vertebrate studies.

Since TDRs are subject to drift in the recording of the depth values, we conducted a 'zero-point calibration' referencing the absolute depth values to the surface (depth 0 m). This procedure involved identifying the shallowest depth recorded each hour (with the two longest dives lasting 27.5 and 15.5 min at least two periods at the surface would occur within each hour) and offsetting all depth values accordingly. Similarly, the SRDL performed an analogous zero-point calibration on board by resetting its internal zero-offset whenever its saltwater switch detected that the device was at the surface.

The TDR and SRDL were attached to a leatherback turtle (curve carapace length 145 cm) by means of a harness (Hays et al. 2004) on Levera Beach, Grenada (12.1°N, 61.4°W) in the West Indies. The harness was attached after the turtle had finished nesting and was returning to the ocean. The deployment began on 27 April 2003 and the equipment was removed on 8 May 2003 when the turtle returned to the nesting beach. The total weight of the harness and devices was <0.5% of the total weight of the turtle and would be expected to have a negligible effect on its behaviour (see Hays et al. 2004 for a detailed critique of the ethical considerations of attaching transmitters and data loggers to leatherback turtles).

Results

Profiles of 229 dives longer than 6 min were successfully received from the SRDL. Mean dive depth ± SD was 114.9 ± 49.6 m ($N = 229$ dives) and mean duration was 10.8 ± 2.8 min ($N = 229$ dives). The residual values relayed for these dives ranged from 0.4 ($N = 2$ dives) to 5.1 ($N = 5$ dives). A visual comparison of the TDR and SRDL data for individual dive profiles of differing residual values (Fig. 1a–j) indicates that the SRDL accurately captured dive profiles even during dives with high residual values.

By interpolation we calculated the depth every second during 85 dives (randomly selecting 10 dives from each residual value with the exception of residual values of 0.4, 4.3 and 5.1 where only two, eight and five dives were available, respectively) in both the TDR and SRDL data sets. This interpolation was made so that both sets of dive profiles then had the same high-resolution timebase, facilitating quantitative comparison. As expected, for dives with a larger residual value, the standard deviation of this depth difference (interpolated SRDL depth minus interpolated TDR depth) was greater (Fig. 2a). However, for all dives, the profiles reconstructed from the SRDL accurately reflected the profiles reconstructed from TDR data (Fig. 2b). This view that the SRDL data accurately reflected the true dive profiles is further reinforced by the strong correlation between the duration and maximum depth for each dive measured by the SRDL and TDR (Fig. 3).

Discussion

We have clearly shown that it is possible to reconstruct dive profiles for marine animals accurately using data relayed via the Argos system. Our study has important implications for behavioural studies being conducted on marine vertebrates around the world, since the Argos system allows remote collection of data from animals over many months or even years regardless of their movements. There is increasing interest in the behaviour of birds (e.g. penguins, albatrosses), mammals (e.g. seal and whales) and reptiles (marine turtles) far away from their breeding sites where data loggers cannot be readily deployed and retrieved. The ability to relay accurate behavioural data via the Argos system therefore has great utility. Similarly, studies with large fish (e.g. tuna, swordfish, sharks) are increasingly trying to relay data via the

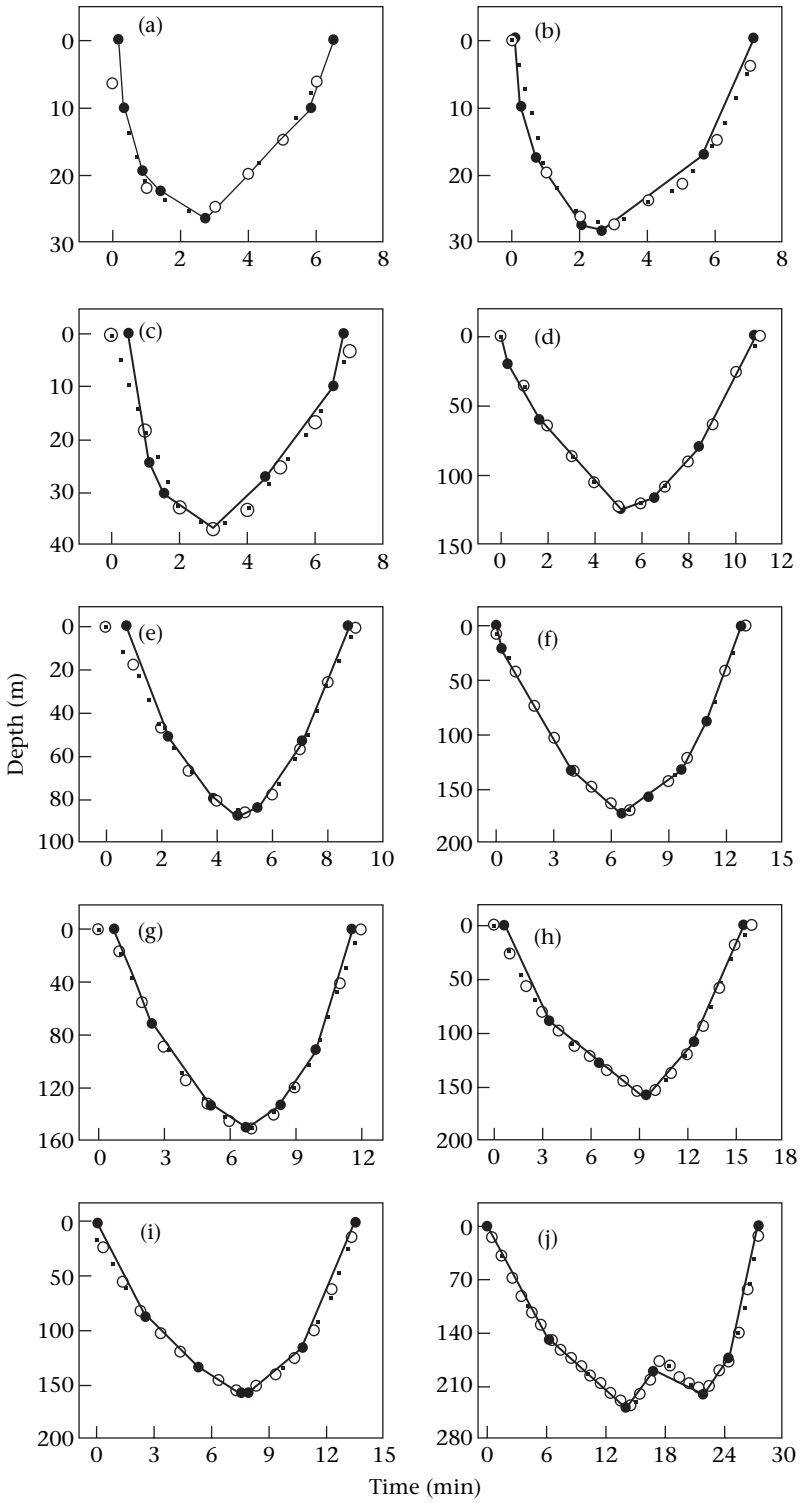

Figure 1. Examples showing the dive profiles reconstructed by the data relayed from the data logger (SRDL) (●, —) and logged by the time–depth recorder (○, - - -) for dives with different residual values. (a–j) Residual values 0.4, 0.6, 0.9, 1.3, 1.7, 2.1, 2.7, 3.5, 4.3 and 5.1, respectively.

Argos system using popoff Argos tags. For example, ongoing tracking within the Tagging of Pacific Pelagics (TOPP) programme involves tracking dozens of vertebrates (fish, mammals, birds and turtles, Block et al. 2003). Similar studies with a range of animals are taking place around the world: in the Southern Ocean (Hindell et al. 2003), Indian Ocean (Guinet et al. 1997), Atlantic (Sims et al. 2003) and Mediterranean (Bentivegna 2002). Service Argos is currently tracking around 1000 marine animals, this number having increased from around 200 animals at any one time in 1995 (A.-M. Breonce, personal communication). In short, the Argos system is being

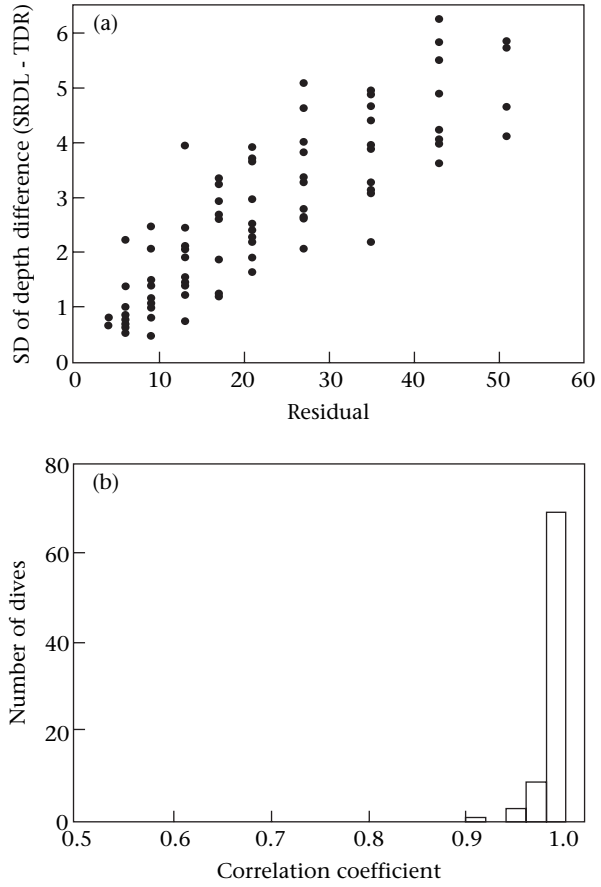

Figure 2. (a) The standard deviation of the depth difference (1-s interpolated SRDL depth minus 1-s interpolated TDR depth) versus the residual value for each dive relayed via the SRDL. (b) The correlation coefficient relating the dive profiles reconstructed from the SRDL and TDR data. SRDL: data logger; TDR: time–depth recorder. See Methods for a description of the residual value transmitted by the SRDL.

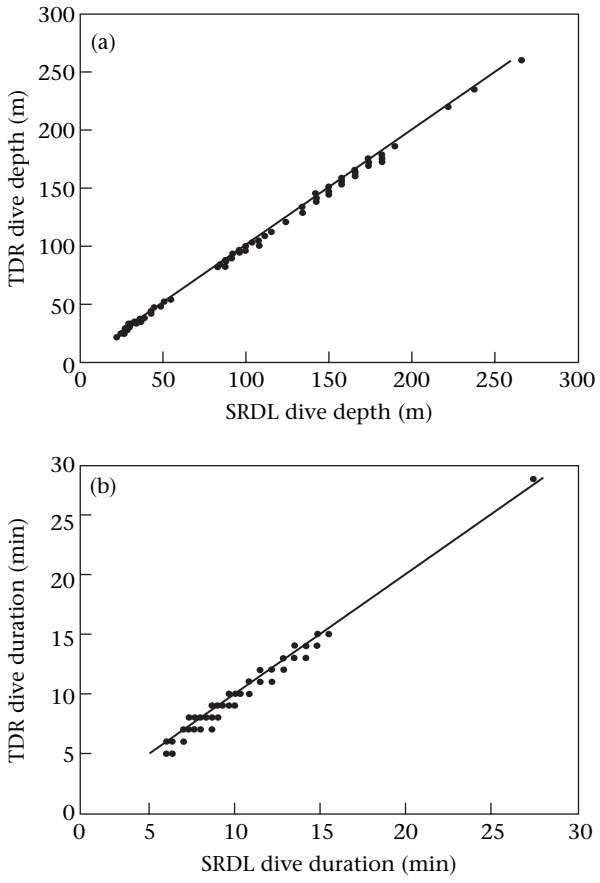

Figure 3. For 229 individual dives the (a) maximum depth and (b) duration measured by the time–depth recorder (TDR) and data logger (SRDL). Lines of equivalence are shown in each case. r^2 values were 0.99 and 0.98, respectively.

more widely used by biologists than ever before, and our study confirms that data collected by this method can be used with confidence. Although we conducted the validation exercise on only one animal, which limits any behavioural observations, the validation exercise itself remains robust since all SRDL units are using the same compression technique to relay dive profiles and onboard zero-point calibration always ensures that sensor drift is not a problem even on long deployments.

Ultimately future developments may bring increased bandwidth within Argos itself or through new satellite systems (e.g. the troubled Iridium and Orbcomm systems), but these have yet to be realized. However, so long as the Argos system remains the mainstay of remote tracking and data collection, the types of data compression tactics prior to transmission that we have outlined here will continue to be important. This system of onboard data compression allows not only dive profiles but also other behavioural (e.g. swim speed) and environmental (e.g. temperature, salinity) parameters to be relayed (Fedak 2004).

The ability to relay dive profile data via Argos opens up the possibility of conducting a new range of behavioural studies. For example, dive profiles may reveal the function of dives (e.g. resting, exploring, feeding etc, Acevedo-Gutierrez et al. 2002; Godley et al. 2003; Ropert-Coudert et al. 2004) and could be used to examine spatiotemporal patterns in marine vertebrate behaviour. Argos-relayed data will allow the testing of theoretical models for how a diver's behaviour can be optimized under varying levels of prey availability (Thompson & Fedak 2001) and will allow general rules to be formulated for the factors driving animal behaviour on macroscales (e.g. movements spanning thousands of kilometres and many months) and microscales (e.g. movement within a distinct area or prey patch over timescales of hours or days). In the future, we envisage that data compression tactics will be applied to the other parameters that are currently being recorded with data loggers (e.g. acceleration, flipper beat frequency, feeding, compass heading) so that they can be relayed remotely via satellite systems with little loss of information.

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