

## All at sea with animal tracks; methodological and analytical solutions for the resolution of movement

Rory P. Wilson<sup>a,\*</sup>, Nikolai Liebsch<sup>b</sup>, Ian M. Davies<sup>c</sup>, Flavio Quintana<sup>d</sup>, Henri Weimerskirch<sup>e</sup>, Sandra Storch<sup>b</sup>, Klaus Lucke<sup>f</sup>, Ursula Siebert<sup>f</sup>, Solvin Zankl<sup>b</sup>, Gabriele Müller<sup>b</sup>, Ilka Zimmer<sup>g</sup>, Alejandro Scolaro<sup>f</sup>, Claudio Campagna<sup>d</sup>, Jochen Plötz<sup>g</sup>, Horst Bornemann<sup>g</sup>, Jonas Teilmann<sup>h</sup>, Clive R. McMahon<sup>a</sup>

<sup>a</sup>*Institute of Environmental Sustainability, University of Wales Swansea, Singleton Park, Swansea, Wales SA2 8PP, UK*

<sup>b</sup>*Leibniz Institut für Meereswissenschaften, Düsterbrookweg 20, D-24105 Kiel, Germany*

<sup>c</sup>*Department of Mathematics, University of Wales Swansea, Singleton Park, Swansea, Wales SA2 8PP, UK*

<sup>d</sup>*Centro Nacional Patagonico (Conicet), Blvd. Brown 3500 (9120), Puerto Madryn, Chubut, Argentina*

<sup>e</sup>*Centre d'Etudes Biologiques de Chizé, Centre National de la Recherche Scientifique, F-79360 Villiers en Bois, France*

<sup>f</sup>*Forschungs- und Technologiezentrum Westküste, Hafentörn, D-25761 Büsum, Germany*

<sup>g</sup>*Alfred Wegener Institute for Polar and Marine Research, Columbusstraße, D-27568 Bremerhaven, Germany*

<sup>h</sup>*National Environment Research Institute Department of Arctic Environment, P.O. Box 358, DK-4000 Roskilde, Denmark*

Accepted 4 November 2006

### Abstract

Determining the movement of marine animals is logistically difficult and is currently primarily based on VHF and satellite-tracking telemetry, GPS, acoustic telemetry, and geolocation, all of which have substantial limitations in accurately locating the fine-scale movements of these animals. A recent development—that of dead-reckoning—is being increasingly used to examine the fine-scale movement of animals underwater. The advantages and drawbacks of this approach are quite different to those incurred by the other methods. This paper considers the advances that dead-reckoning can bring to the study of the often cryptic movement and behaviour of marine animals at sea. Methods used in determining position via dead-reckoning are presented and consideration is given to results derived from the use of dead-reckoning on cetaceans, pinnipeds, penguins and sea turtles; these are complemented by data on cormorants and albatrosses acquired using GPS systems. Suggestions are made as to how movement data derived from these devices can be analysed using indices that allow interpretation over a large variety of temporal and spatial scales.

© 2007 Elsevier Ltd. All rights reserved.

**Keywords:** Data loggers; Dead-reckoning; Habitat selection; Navigation; Telemetry; Track tortuosity

### 1. Introduction

There are essentially six methods for determining the position of marine animals at sea when they cannot be observed directly. Four of these will only work if the animal is at the surface for some period;

\*Corresponding author. Tel.: +44 1792 295376;  
fax: +44 1792 295344.

E-mail address: [r.p.wilson@swansea.ac.uk](mailto:r.p.wilson@swansea.ac.uk) (R.P. Wilson).

VHF telemetry (Hooker et al., 2002 and references therein), satellite tracking telemetry (Ferraroli et al., 2004; Hays et al., 2004a; Jouventin and Weimerskirch, 1990; Sims et al., 2005), GPS technology (Weimerskirch et al., 2005), and geolocation or global location sensing (e.g., Block et al., 2001; Hill, 1994; Wilson et al., 1994). Only two methods work underwater, these being acoustic telemetry (e.g., Hindell et al., 2002) and dead-reckoning (Wilson and Wilson, 1988). Acoustic telemetry necessitates that receivers be within a few hundred metres of the animal to be tracked so that fast and widely ranging species are difficult to access with this method. Dead-reckoning necessitates that animal speed, heading and change in depth (or swim angle) be known so that the three-dimensional movements of the animal can be calculated by use of vectors. Dead-reckoning also requires that either the device be recovered to access the data, or that the data be transmitted at the end of the wearing period. Although earlier attempts to use dead-reckoning principles were primitive (Wilson and Wilson, 1988), advances in solid state technology, particularly as regards to sensors and memories (Fedak, 2004; Kooyman, 2004), have meant that dead-reckoning is now coming of age with highly complex systems being used on a variety of air-breathing marine vertebrates (e.g., Davis et al., 1999; Wilson and Liebsch, 2003; Johnson and Tyack, 2003; Mitani et al., 2003; Zimmer et al., 2005).

The particular forte in dead-reckoning is that it produces temporally finely-resolved, regular, sequential positional data with no gaps (Wilson et al., 2002a), something that is generally, otherwise, particularly difficult to acquire in studies of marine vertebrates. As such, dead-reckoning is a unique tool for describing animal movements.

Effective descriptions of the foraging behaviour of animals should be able to identify systematic patterns (or even the lack of them) and ultimately allude to the adaptive significance of such movements (e.g., Bradshaw et al., 2004; Sims et al., 2005). Although there are extensive mathematical treatises devoted to e.g., fractal analysis (Fritz et al., 2003), sinuosity indices (Benhamou, 2004), and first passage times (Frair et al., 2005) many of these are intuitively difficult to access, which makes understanding for field biologists problematic. Such approaches are also often designed to deal with poor-quality positional data, this being dictated by the logistics of the study of the animals in the field. Finally, these methods generally look at e.g.,

changes in track tortuosity over various scales without due consideration of how patterns in space use vary over time.

In this work, we describe some of the dead-reckoning systems that we have used, and present examples of data that show the different types of movement exhibited by a variety of species we have studied. We also propose a new method to help in the analysis of animal movement that is particularly appropriate for data gathered by dead-reckoning because it benefits from the temporally regularly spaced data. This method allows workers to visualise the types of movement used by their study species with temporal and spatial elements in the foraging tracks clearly separated so that species-specific patterns become apparent. The dead-reckoning data are complemented by data on animal positions taken by using GPS logging systems on marine animals that spend extensive periods above the surface. This should serve as a useful reference for future studies and help define how dead-reckoning (and GPS) data can be used in a behavioural, rather than just a positional context.

## 2. Methods

### 2.1. Device deployments

This work presents location data gathered from 11 species of marine vertebrate including; turtles, birds and mammals. We also present some data from terrestrial applications (dogs, humans). Rather than presenting the details of all deployments here, relevant, necessary information is provided in the results. In essence, though, all positional data were derived from either dead-reckoning loggers or GPS loggers, and some data are also presented using accelerometer loggers. All units were programmed using computers with the appropriate interface, and dead-reckoning data were treated by specially written software (MT-Route and Route10; Jensen Software Systems, Laboe, Germany) to allow calculation of animal movement (see Section 2.3).

### 2.2. Sensors used in dead-reckoners

#### 2.2.1. Speed

Speed was sensed using paddle-wheels (Wilson et al., 1993), differential pressure sensors incorporating Prandtl tubes (Wilson et al., 2002a, b), variation in signal from two absolute pressure sensors (one of which sensed simple hydrostatic

pressure while the other sensed hydrostatic pressure plus water pressure resulting from movement (cf. Wilson et al., 2004)), or Hall effect magnetometers (Wilson and Wilson, 1988; Kreye, 2003). Most of these systems only began working effectively at speeds in excess of 0.4 m/s and were good to within 0.1 m/s after calibration on models in a tank (cf. Wilson et al., 2004). This nominally limits their use to species that rarely travel at speeds less than this although we modified sensitivities accordingly for the slower-swimming species such as turtles (Kreye, 2003).

### 2.2.2. Heading

Heading was determined using one of two compass types: a mechanical system and a solid-state system. The mechanical system consisted of three Hall sensors integrated in a miniature, fluid-filled, three-dimensional ship's compass to indicate animal direction and angle of animal inclination. Each Hall sensor was located on the outside of the containing sphere and placed at 90° to the others. The position of a powerful rare earth magnet, driving a buoyant inner sphere to be permanently orientated in a North-South direction, was determined by the Hall sensors reacting to the different magnetic field strengths produced by the varying positions (for a similar approach see Hochscheid and Wilson, 1999). During extensive calibrations, a matrix of Hall sensor output was stored against pitch, tilt and roll angle of the compass exposed to the magnetic field at the site of deployment. Steps of 10° were used in the calibration and interpolation was used to derive a resolution of 2° in the final matrix. In the derivation of animal heading, the computer programme consulted the matrix to find the best solution corresponding to the recordings of the three Hall sensors. In tests, we found that heading could be determined to within 3°.

The solid state compass (Honeywell, Plymouth, USA) consisted of a tri-axial magnetometer that sensed the magnetic field strength of the earth so that, after taking into account sensor angle (derived from pitch and roll sensors in the dead-reckoner), animal heading could be determined (this procedure is outlined in Mitani et al., 2003). The manufacturers state that using this system, heading can be determined to within 1°.

### 2.2.3. Depth

Depth was sensed using medium-separated pressure sensors (Keller AG, St Gallerstrasse 119,

Winterthur, Switzerland) designed to operate within the ranges of 0–10, 0–20 or 0–40 Bar, depending on the animal concerned, with resolution that varied between 8 and 16 bit. In most of our applications the depth could thus be resolved to better than 0.5 m.

### 2.3. Dead-reckoning calculations

We noted the position of animals equipped with dead-reckoners at the time they were released into the wild using GPS. Absolute distances moved over the sampling intervals were derived from the measurements of speed and the horizontal distance moved over any one sample interval was derived from the absolute distance  $D_j$  and pitch angle of  $\alpha_j$ , (between times  $t_j$  and  $t_{j+1}$ ) according to:

$$d_j = D_j \cos \alpha_j. \quad (1)$$

Assuming the animal's position at  $t_j$  to be  $(x_j, y_j)$ , and its heading to be  $\theta_j$ , then its position at  $t_{j+1}$  was calculated via:

$$(x_{j+1}, y_{j+1}) = (x_j + d_j \sin \theta_j, y_j + d_j \cos \theta_j). \quad (2)$$

Substituting from (1) the position at  $t_{j+1}$  is

$$(x_{j+1}, y_{j+1}) = (x_j + D_j \cos \alpha_j \sin \theta_j, y_j + D_j \cos \alpha_j \cos \theta_j). \quad (3)$$

This process was carried out starting with step one at  $t_0 = 0$  through to the last position, with the animal's position being changed in a cumulative manner. Where the end position of the equipped animal was known, taken to be  $(x_{\text{realend}}, y_{\text{realend}})$ , the calculated position  $(x_{\text{calcend}}, y_{\text{calcend}})$  could be compared to give the total positional error as

$$(x_{\text{realend}}, y_{\text{realend}}) - (x_{\text{calcend}}, y_{\text{calcend}}). \quad (4)$$

Assuming drift to be constant over time, the error per measurement interval was taken to be

$$(x_{\text{corr}}, y_{\text{corr}}) = ((x_{\text{realend}}, y_{\text{realend}}) - (x_{\text{calcend}}, y_{\text{calcend}}))/n. \quad (5)$$

Using Eqs. (3) and (5), we corrected the best estimate for animal position at any time  $t_{j+1}$  to be:

$$(\tilde{x}_{j+1}, \tilde{y}_{j+1}) = (x_j + D_j \cos \alpha_j \sin \theta_j + jx_{\text{corr}}, y_j + D_j \cos \alpha_j \cos \theta_j + jy_{\text{corr}}) \quad (6)$$

[equivalent to recalculating the positions using the algorithm

$$(x_{j+1}, y_{j+1}) = (x_j + D_j \cos \alpha_j \sin \theta_j + x_{\text{corr}}, y_j + D_j \cos \alpha_j \cos \theta_j + y_{\text{corr}})].$$

Following this analysis, tracks were produced that consisted of  $x$ ,  $y$  and  $z$  co-ordinates in metres from the start point, separated at intervals that corresponded to the intervals at which the data were logged (varying between 0.2 and 10 s).

#### 2.4. Analytical methods for examination of track tortuosity

We initially produced a definition of two-dimensional track tortuosity based on the horizontal straight line distance travelled by an animal over a defined time period (encompassing  $m$  sampling periods) divided by the total horizontal distance travelled calculated by summing the horizontal distance travelled during each measurement interval from times  $t_j$  to  $t_{j+m}$ . We only applied this process where animals were known to be travelling rather than resting in one spot as evidenced by speed and/or depth sensors.

Mathematically, this is:

$$\begin{aligned} & |(\tilde{x}_{j+m}, \tilde{y}_{j+m}) - (\tilde{x}_j, \tilde{y}_j)| / \sum_{k=0}^{m-1}, \text{ or} \\ & |(\tilde{x}_{j+m}, \tilde{y}_{j+m}) - (\tilde{x}_j, \tilde{y}_j)| / \sum_{k=0}^{m-1} |d_{j+k}(\sin \theta_{j+k}, \cos \theta_{j+k}) \\ & \quad + (x_{\text{corr}}, y_{\text{corr}})| \end{aligned} \quad (7)$$

for the raw and corrected data, respectively.

In order to define some measure of Area Interest Index (AII), we subtracted this value from 1 so that straight line travelling had values of 0 and circular movement within the specified time interval had a value of 1 (Fig. 1). Thus

$$\begin{aligned} \text{AII} = 1 - & |(\tilde{x}_{j+m}, \tilde{y}_{j+m}) - (\tilde{x}_j, \tilde{y}_j)| / \sum_{k=0}^{m-1} |d_{j+k}(\sin \theta_{j+k}, \cos \theta_{j+k}) \\ & + (x_{\text{corr}}, y_{\text{corr}})|. \end{aligned} \quad (8)$$

We set  $m = 2$  in all future calculations of AII referred to in this work. This approach shows how the tortuosity of tracks varies with time but does not adequately allow the variation in tortuosity of tracks as a function of scale to be assessed if step length remains constant because high levels of small-scale tortuosity impact the lower term in Eq. (8) even if  $m$  is increased. To deal with this problem  $x$ ,  $y$  positional data were run once to calculate the AII before being progressively thinned to increase the step length (Fig. 1). The AII

calculation was then re-run while holding  $m$  constant at 2. Thus, although the absolute integer value of  $m$  remained constant, its effective value in terms of time varied, becoming larger with increased thinning. In order for the values of AII from each run to be completely independent of the preceding run, the thinning out process nominally involved removing every other point at each subsequent stage. Thus, if the sample interval was  $i$ , the effective step length was  $i$ ,  $2i$ ,  $4i$ ,  $8i$ , ... in four runs of increasing scale assessment (Fig. 1). Note, that where  $m > 2$ , problems can occur due to aliasing in the data because, by repeatedly sub-sampling the data, without pre-filtering, high-frequency processes can be aliased, causing them to appear as lower-frequency processes. The solution to this is to filter the data before sub-sampling. Where every other point is to be sub-sampled, for example, the filter should be implemented to remove variation in the top half of the pass-band (by weighted averaging of spatial locations prior to sub-sampling). Finally, we note that our procedure, as described, appears to throw many of the data away. However, by beginning the procedure after the first time interval, a second estimate of the high-frequency AII can be derived, albeit relating to a slightly later period. The next lower-frequency AII can be similarly estimated for any of the next three intervals, for example. These estimates can then be used with a smoothing procedure to provide the best estimate at any one time for a given frequency.

The procedure described above produced the data necessary for a three-dimensional matrix of AII against time as a function of scale and these data were subsequently gridded using the program Surfer (Golden Software) according to the default setting using kriging as the methodology. We note here that the precise method by which this gridding occurs will affect the resultant picture substantially and this should be given careful thought (although discussion here is not warranted). The subsequent plot was also undertaken using Surfer (Fig. 1, right hand side) with the plots being improved by thinning data less than by simply removing half the points at each stage, although the interdependence of adjacent points on the surface must be borne in mind.

### 3. Results

We have regularly spaced, finely resolved data on movement in free-living animals from a total of 11 species. Inspection of the simple horizontal

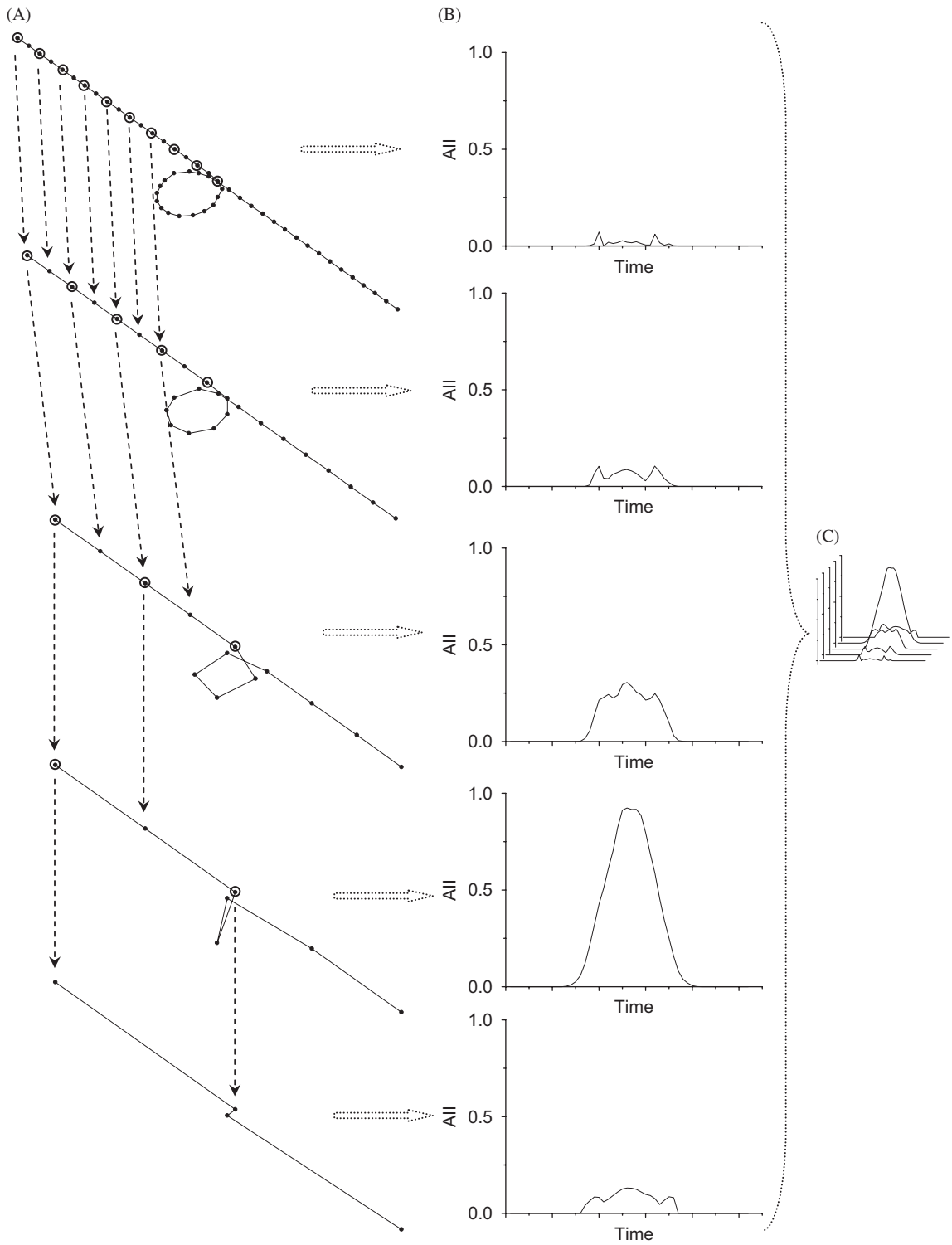


Fig. 1. (A) Theoretical path of an animal showing a loop in the overall straight course but subject to increasing thinning (top to bottom) by deletion of every other point so that resolution of movement becomes increasingly coarse. (B) Shows the AII ( $m = 2$ ) for the various tracks. Note that the highest values occur when 16 points have been deleted and that the loop is composed of ca. 16 points in the finest resolution. (C) Shows a 3-d plot of AII (vertical axis) versus time and degree of data reduction (scale).

displacement in these shows the substantial variation in path tortuosity over time and over the different scales (e.g., Fig. 2). The representation of such movements as an AII in a scale-based diagram in the form of a contour plot (Fig. 3) shows how different scales of tortuosity can be presented with an equal weighting and how this varies over time.

Consideration of contour plots of AII versus time and scale in different species shows that all species have periods of straight line travel over almost all scales and these periods are often separated by increases in AII also over all scales considered on the  $y$ -axis (these appear as vertical lines in the plots although these lines will be over-exaggerated due to

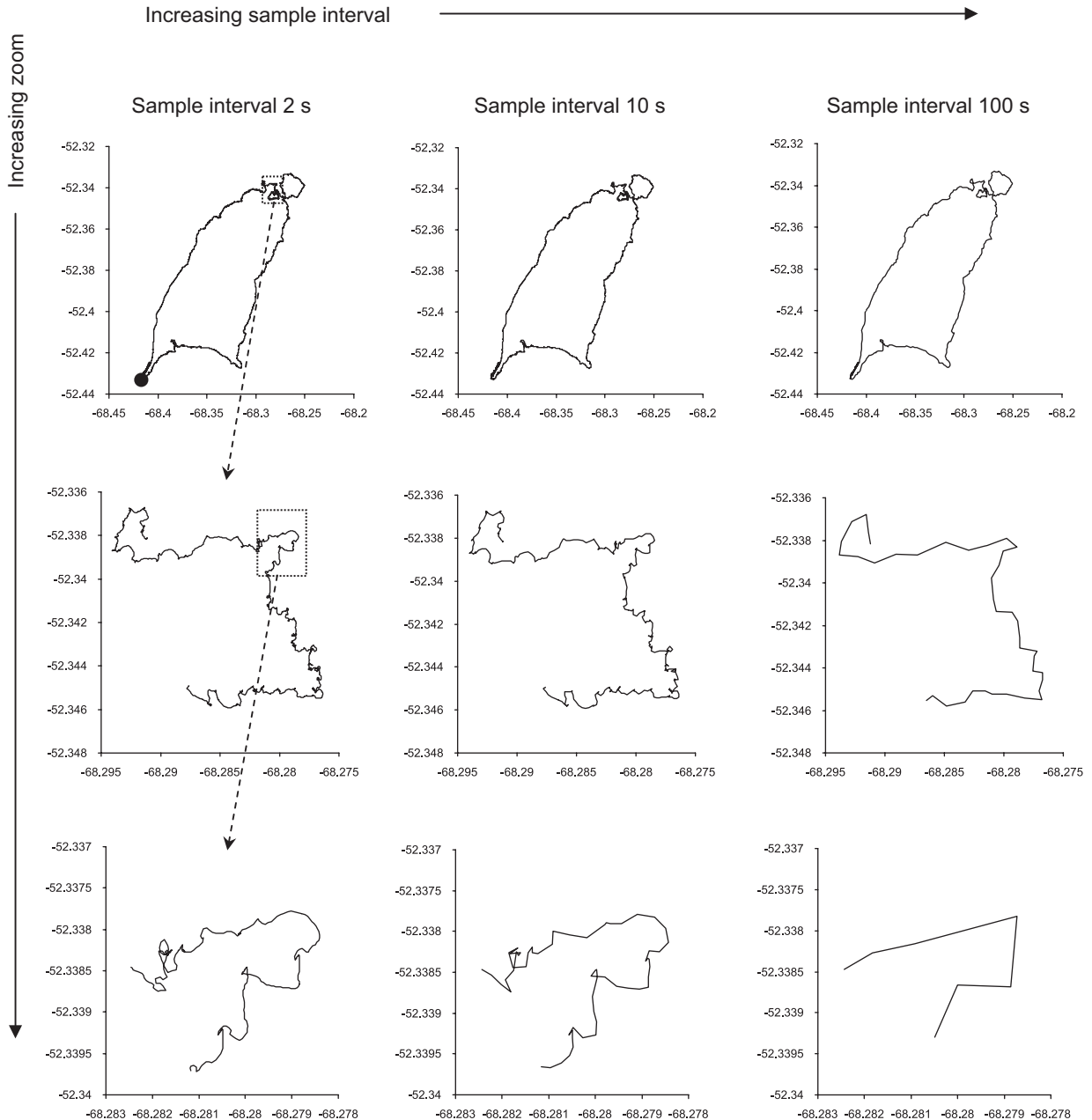


Fig. 2. Track of a Magellanic Penguin *Spheniscus magellanicus* equipped with a dead reckoner and foraging from a colony at Cabo Virgenes, Santa Cruz, Argentina. The graphs show the effect of sample interval on apparent path tortuosity (left to right) and the degree of convolution of the route according to the scale over which it is considered. The circle in the left hand corner of the top graph shows the point of departure and arrival of the bird at the colony.



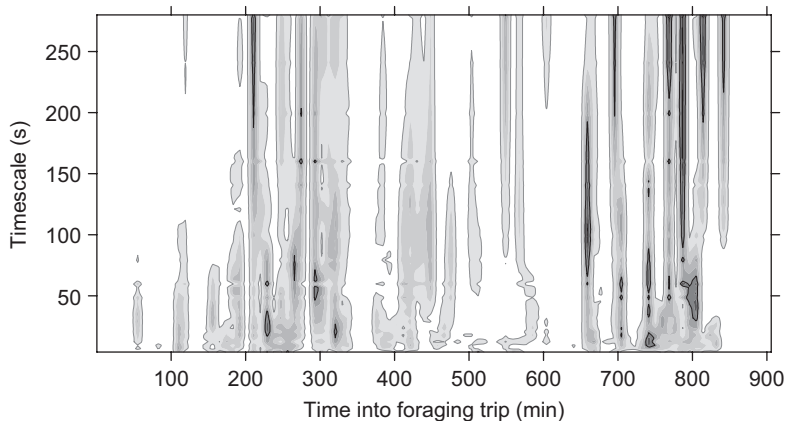


Fig. 3. Contour plot of the Area Interest Index (AII) versus time as a function of (time) scale of a foraging track of a Magellanic Penguin (shown in Fig. 2). AIIs of  $<0.1$  are shown by white areas and increasing shading shows increasingly convoluted tracks. AIIs in excess of 0.5 are delineated by black lines. Shading levels correspond to AII intervals of 0.1.

the large difference in scale between  $x$ - and  $y$ -axes) (Fig. 4). Within the examples shown there are obvious cases of species that have the majority of the displayed AII surface dedicated to straight line travel (the porpoise, sea lion and seal), while others have greater proportions of convoluted tracks (the penguins) and one (the turtle) even has a predominantly convoluted track at the scale shown (Fig. 4). This last case is to be expected because the animal was engaged in an inter-nesting interval and moved little. Other than this, all tracks were derived from animals known to be foraging. Clearly marked deviations from straight-line travel (shaded regions in the AII contour plots) correspond to ‘convolution events’, and can be defined by particular shapes or forms, most of which appear as vertical bars (see above). Otherwise, deviations may appear as relatively rounded shapes in the AII contour plots, something that is particularly easy to see when the data are gridded with fine temporal and spatial resolution (Fig. 5). In some species, such as the Wandering albatross, these points appear, at times, with almost systematic regularity.

Aside from data on animals that uniquely travel by swimming or flying (Figs. 3–5), we have derived AII contour plots with data from Imperial cormorants that travel by both flying and swimming (Fig. 6). The plots show markedly different AIIs according to travel mode, with almost all extended flight sections being in a straight line (Fig. 6B) whereas swimming periods are generally tortuous at very small scales although at larger scales they too may be in straight lines (Fig. 6 Section B).

Our primary aim in this treatise was to develop a method to examine animal movement in the two-dimensional horizontal plane. It is worth noting, however, that this process can be performed on data in three-dimensional space or in a single dimension such as depth.

## 4. Discussion

### 4.1. Errors in dead-reckoning

Dead-reckoning for animals necessitates that three elements be recorded; animal speed, animal heading and animal position in the vertical axis. In addition, the animal’s position must be known at least once during the period when its movement is being monitored so that relative calculated coordinates can be ascribed to position. Typically, the animal’s position is known at the moment the animal is equipped and released into the wild at time  $t = 0$ , so that the position at  $t = 1$  is given by consideration of this start position modified by the distance vectors derived from animal speed between  $t = 0$  and  $t = 1$  and the heading and pitch angle (this latter being derived from the change in animal height (or depth) between  $t = 0$  and 1). A primary element in determining overall route calculations in dead-reckoning resides with the accuracy of the primary logged parameters of speed, depth and heading.

#### 4.1.1. Speed

The accurate measurement of speed is a critical element in determination of routes determined using

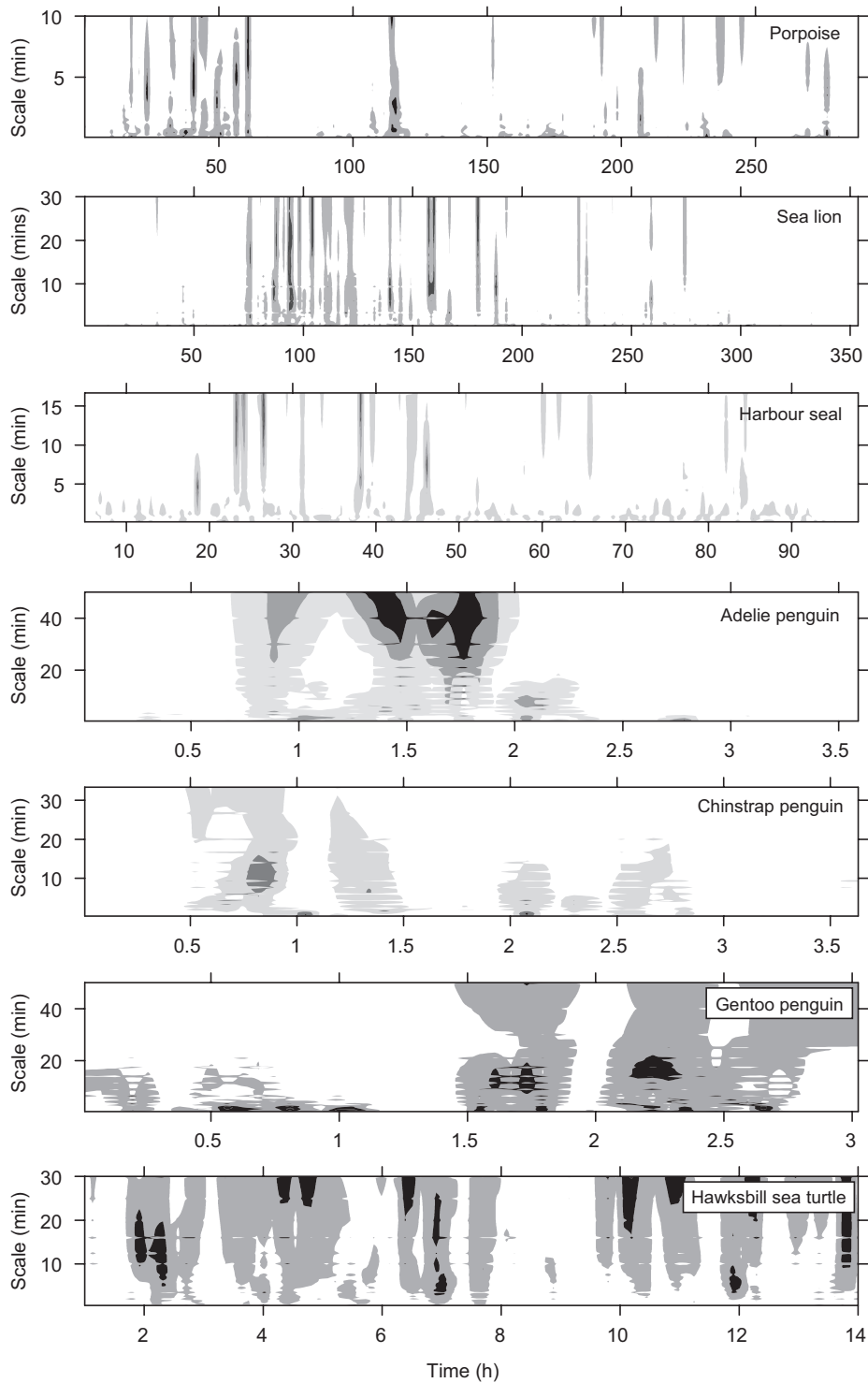


Fig. 4. AII contour plots for seven different marine animals. Contour intervals are the same in all species with the white surfaces corresponding to AII values of less than 0.1, with levels increasing by values of 0.25 in stages beyond this and depicted by increasing shading. All species were equipped with dead-reckoners to determine movements although sampling intervals varied. Conditions were: Harbour Porpoise *Phocaena phocaena* equipped in the Baltic (2001), sample interval 6 s; South American Sea Lion *Otaria flavescens* equipped at Peninsula Valdes, Argentina (2004), sample interval 10 s; Harbour Seal *Phoca vitulina*, equipped in the North Sea (2004), sample interval 10 s; Adélie Penguin *Pygoscelis adeliae*, Chinstrap Penguin *Pygoscelis antarctica* and Gentoo Penguin *Pygoscelis papua* equipped at King George Island, Antarctica (1992), sample interval 10 s; Hawksbill Turtle *Eretmochelys imbricata*, equipped in the Caribbean (1998), sample interval 15 s.



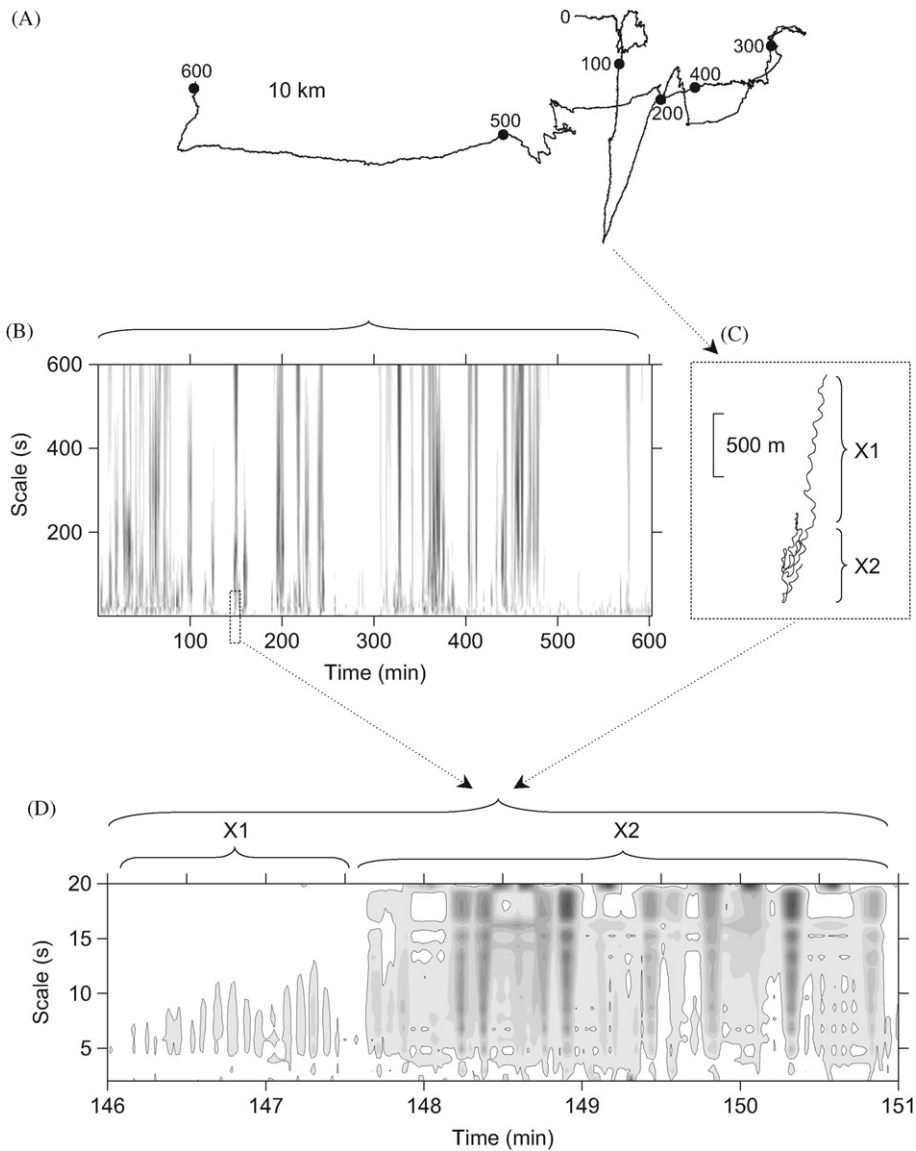


Fig. 5. (A) Section of a flight of a Wandering Albatross *Diomedea exulans* equipped at Possession Island, southern Indian Ocean with the time travelling at  $> 2$  m/s shown in minutes with (B) the corresponding AII contour plot. The insets in (A) and (B) are shown expanded in (C) and (D), respectively. Note how repetitive patterns from dynamic soaring (X1 in (C)) give a characteristic AII pattern (X1 in (D)) with the minimum turn radius of the bird dictating how far down the scale the contours can extend. AIIs of  $< 0.1$  are shown in white and increasing density steps = 0.1.

dead-reckoning. Systematic under-, or over-estimation leads to reduced or expanded moved ranges/distances which leads to incorrect absolute positions although it does not affect elements such as the tortuosity of tracks. There is remarkable variation in the types of speed sensors used by different groups working on marine animals and options include paddle wheels (Ponganis et al., 1990; Sundstrom and Gruber, 1998), propellers (Ropert-

Coudert et al., 2002; Yoda et al., 2001), turbines (Eckert, 2002), differential pressure sensors (including those using Prandtl tubes) (Wilson et al., 2002a, b) and absolute pressure sensors (Wilson et al., 2004), Hall effect magnetometers (Kreye, 2003) and piezo-resistive sensors (R.P. Wilson, Unpubl. data). All methods that involve moving parts have a stall speed below which they do not work, and this is typically 0.3 m/s so errors can be

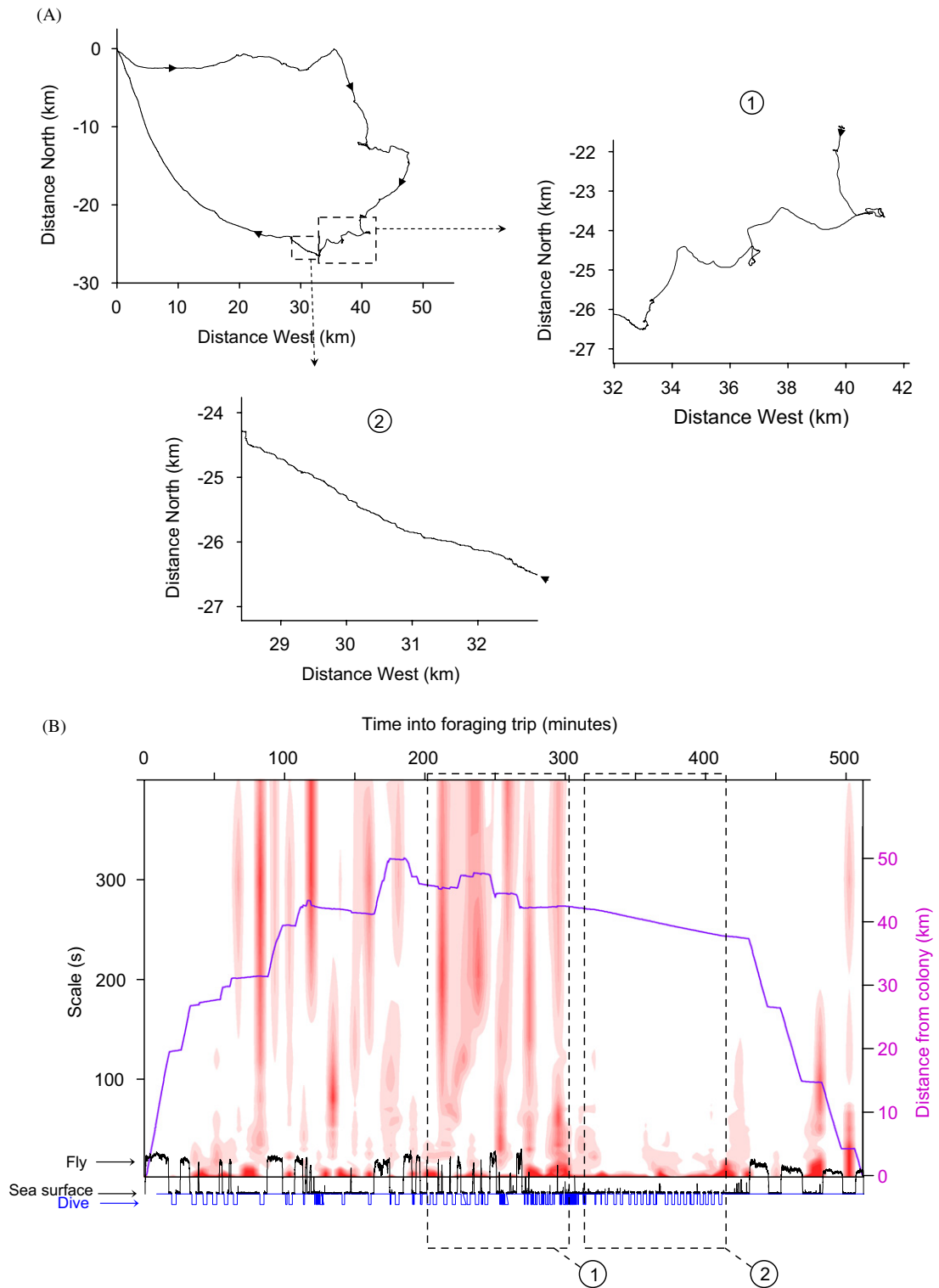


Fig. 6. (A) Movements of an Imperial Cormorant *Phalacrocorax atriceps* made during a foraging trip from a colony at Punta León, Chubut, Argentina (2004) as determined by a GPS logger recording at intervals of 1 s. The position of the bird underwater was simply calculated by interpolating linearly between GPS fixes at the surface between dives. Sections 1 and 2 show zooms, which can be put into perspective by looking at (B).

substantial. A suggested alternative that does away with this would use the Doppler shift (Kreye, 2003), although to our knowledge this principle has not yet been used on animals. Probably the most serious error in measurement of speed stems from inappropriate calibration. The speed of water flow over an animal varies with animal size and shape and position of the speed sensor (Bannasch et al., 1994) so transducers that measure speed should be calibrated on life-size models. Even so, water flow may differ to that over real animals (Carpenter et al., 2000). This problem can be negated by having loggers with high-resolution tilt sensors (e.g., Mitani et al., 2003) and pressure transducers so that the speed component of a dive can be calculated by equating the rate of change of depth with dive angle and this can be regressed against the value recorded for speed to produce a relationship between speed sensor output and real speed. The value of this approach is that the process can be used at any time when the animal is ascending or descending the water column (i.e., there is potential from every dive) (Blackwell et al., 1999) and the process can be repeated at intervals through the logged period to ascertain that there is no change in the calibration.

Theoretically, there is no reason why dead-reckoners should not be used on terrestrial animals where they would be particularly useful in animals living in environments that do not lend themselves to GPS, such as thick vegetation (Frair et al., 2004) or where power requirements make a high frequency of fixes difficult (Anderson and Lindzey, 2003). The major problem here is the determination of speed or effective distance travelled. Speed can theoretically be determined via acceleration (cf. Yoda et al., 2001), but in practice this is subject to substantial errors so that dead-reckoning does not work (Springer, 1992). The approach currently being adopted is that of analysis of animal strides determined via accelerometry (Fig. 7A) because stride length equates with both stride frequency and measured amplitudes in the acceleration wave signal (Fig. 7B). It is likely, however, that such measures will have to consider individual morphology and, despite this, that terrestrial dead-reckoners will be subject to errors. The extent of these errors will be most easily apparent after trials. In its favour, however, terrestrial dead-reckoning is not subject to drift errors, which may be a problem in aquatic animals and is particularly grave in flying species (Dallantonia et al., 1995).

#### 4.1.2. *Depth and animal pitch*

Errors in depth are of little concern in dead-reckoning because depth transducers tend to be highly accurate (usually accurate to within a fraction of a metre; Hays et al., 2004b). Moreover, every depth reading can be taken as an independent event, a mono-dimensional equivalent of a GPS fix. The greatest consequence of inaccurate depth measurement relates to determination of speed (in calibrations for speed sensors where the change in depth over time is related to body angle—see Section 4.1.1). In fact, values for speed taken from a calibration can be used in tandem with recorded data on pitch as well as rate of change of depth in a triangle of elements to examine variance and consistency in all three parameters. Perhaps one of the greatest errors in this approach lies in apparent inconsistencies between body pitch angles and rate of change of depth at a given speed because the device actually only measures device pitch angles rather than animal pitch angles and if device orientation does not represent the true longitudinal axis of the animal errors will arise. A way around this problem is to look for sections of the data where there is no depth change between two consecutive readings before examining the pitch recorded from the instrument at this time. The difference in the recorded pitch from the device and the actual pitch of the animal represents the offset with which all pitch measurements must be corrected so that device data truly represent the animal pitch (Sato et al., 2003).

#### 4.1.3. *Compass heading*

The manufacturers of solid-state compasses state that their systems can resolve heading to within 1°. This assumes virtually perfect information on compass orientation (pitch and roll) because solid state compasses record tri-axial magnetic field intensity, which is then put into perspective by consideration of compass sensor orientation with respect to gravity and magnetic declination. Both magnetic field strength and declination vary with location so that solid-state compasses produce outputs that vary accordingly. However, since the output of any one of the tri-axial magnetic field strength sensors depends directly on the angle and the strength of the impinging magnetic field, a simple calibration at the site of deployment should suffice to allow device orientation to be calculated. Where animals tracked using dead-reckoning travel extensively, web sites, such as

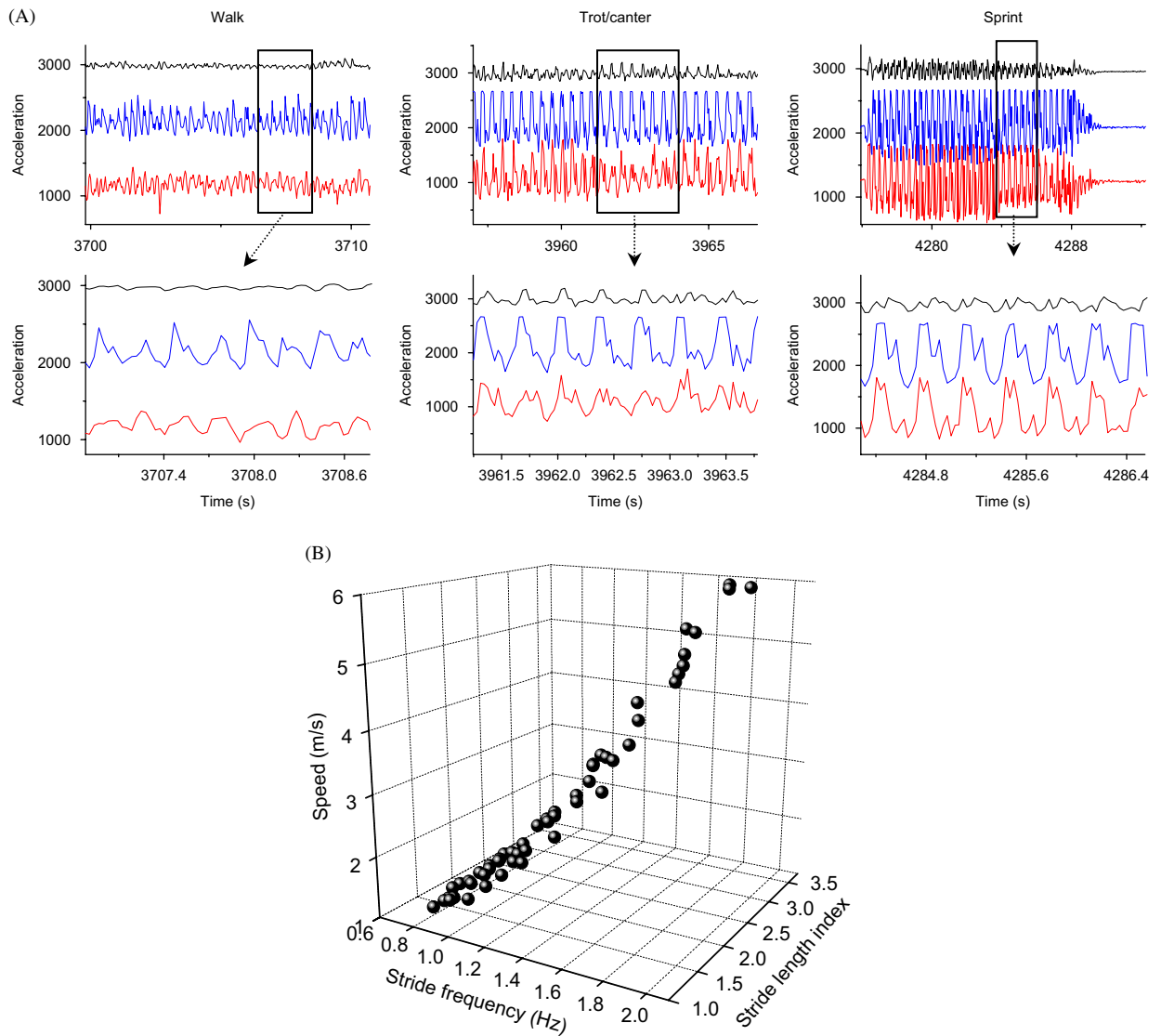


Fig. 7. (A) Changes in surge (black line), heave (blue line) and sway (red line) acceleration recorded by a logger mounted on a collar of a 15 kg border collie *Canis familiaris* sampling at 32 Hz during different speeds of movement. Note that acceleration units are relative and offset from each other to highlight trends. (B) Measured speed in 12 humans travelling at different velocities as a function of stride frequency and length derived from logger accelerometry data. Although the volunteers were both male and female and showed high morphological variance (outside leg dimensions 94–112 cm) the 3D plot shows a remarkably tight relationship.

<http://www.ngdc.noaa.gov/seg/geomag/magfield.shtml> can be used to derive magnetic field declinations and intensities and outputs interpreted accordingly. Implicit in determination of animal heading is that both the compass sensor and the body orientation sensor are perfectly aligned on the circuit board, which can be achieved with careful engineering or can be corrected after careful calibration. However, the ability of the compass sensor to provide a true animal heading also depends on the extent to which device orientation reflects animal orientation. In

fact, it is not a trivial matter to fix a device to an animal so that it faces exactly forward. While errors in device pitch can be corrected, problems with device heading not representing those of the animal are more difficult to assess (Fig. 8) but can be alluded to by careful observation of the way the device sits on the animal after it has been released.

Finally, studies on animals close to the magnetic poles may not be able to use dead-reckoning since the horizontal component of the magnetic field becomes negligible, and difficulties may also arise

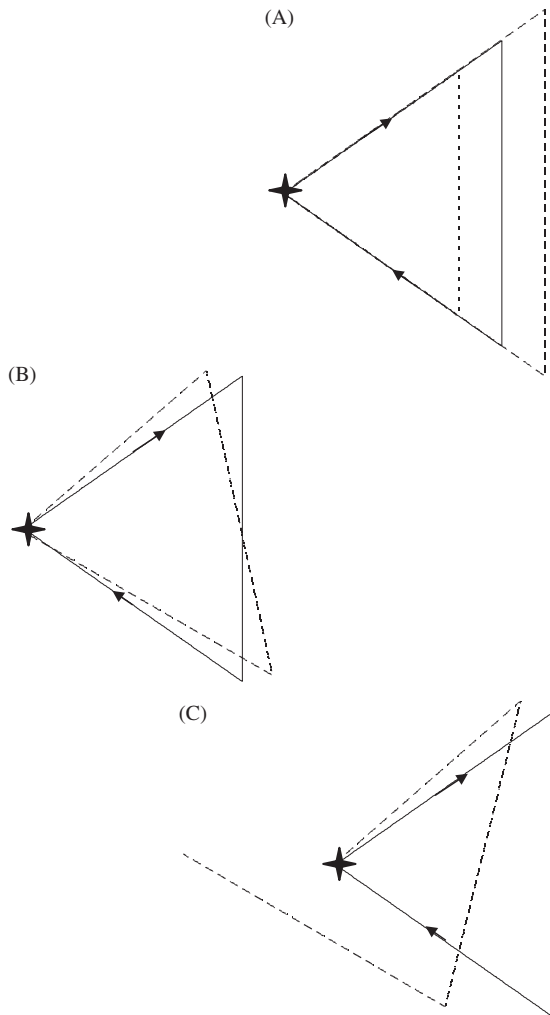


Fig. 8. A theoretical route calculated for an animal starting from the point shown by a cross and based on dead-reckoning (swim speed 1 m/s), shown in continuous lines in all figures, has been subject to errors to show the effect on route calculations: (A) Inaccurately estimated speed, with dashed line showing over-estimated ( $v = 1.2$  m/s), and dotted line under-estimated ( $v = 0.8$  m/s), speeds. (B) Heading misrepresented by  $5^\circ$  due to skew device attachment to the animal. (C) Drift due to a transverse current flowing at 0.1 m/s from East to West.

when using such systems in areas with magnetic anomalies.

## 4.2. Route calculation

### 4.2.1. Environmental errors and methods to reduce them

Errors in the accuracy of any of the sensors described above are most serious if they are systematic, although if the extent of sensor error is

known most problems can be resolved by appropriate modified calibrations (cf. Fig. 8). However, the environment also acts to produce systematic errors. Thus, animals operating in moveable media, such as flying birds (subject to wind) or swimming species (subject to currents), can drift off calculated positions. A primary indication that this has happened occurs when two defined, and known, points on the track (such as start and end points) do not coincide with the calculated positions. The problem can then be reduced by determining the difference in space between the defined points and correcting the points between to accord (see Eq. (6)). This process assumes linear drift over time, though, which may not be the case. Knowledge of local current or wind conditions may help here although an increased number of independent true fixes, such as via GPS, is the ideal solution with, ultimately, the most accurate routes calculated by dead-reckoning being those with the highest incidence of GPS positional fixes. Such fixes can correct for positioning errors described above as well as indicating the extent of the errors. GPS fixes also highlight where temporary sensor malfunction may occur, speed sensors being particularly susceptible to this due to blockage by material. The combination of dead-reckoning with GPS promises to be a particularly powerful methodology for determining animal tracks since GPS-derived data suffer only from a virtually invariant, known positional error per fix, while dead-reckoning, although subject to cumulative errors, can fill in for periods when GPS technology does not work, such as underwater. Where GPS technology does not work at all, consideration of the depths reached by equipped diving animals may help refine estimates of position if the bathymetry is accurately known (working on the principal that no animal can dive deeper than the bottom).

This process can be even more refined in terrestrial animals since they can only move over a two-dimensional surface. Thus, body angles and directions and changes in height must conform to the topography of the terrain so that this also could be used as an independent measure of the correct functioning of the system.

The considerations above are most important with respect to absolute animal position. However, even when long deployments of dead-reckoners result in so much error (e.g., via differential drift) that accurate true positions cannot be resolved, the relative movement displayed by the animal for

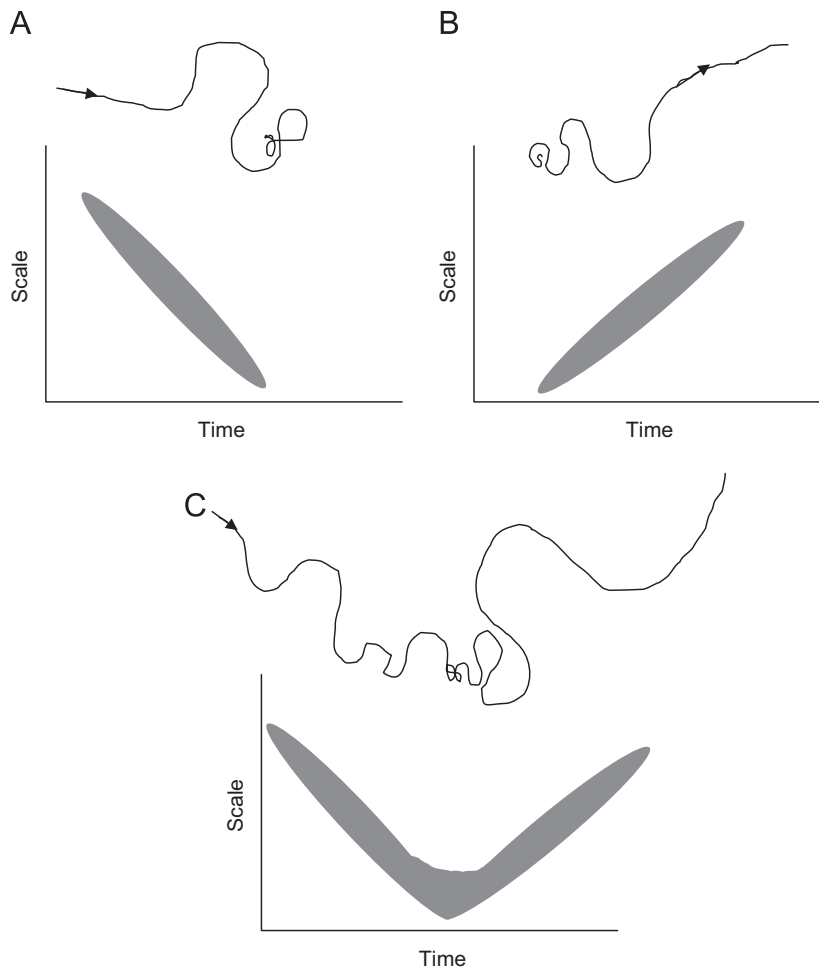


Fig. 9. Schematic view of how particular travel features are displayed in AII contour plots. (A) Shows an example of movement of an animal localising its prey by e.g. scent; (B) Shows an example of how an animal that has localised prey might subsequently search the environs by gradually increasing its search radius and (C) Shows how the two processes might be combined.

periods during that deployment still can be usefully assessed in a behavioural context provided the time interval over which the analysis is conducted is not excessive.

Overall, we believe dead-reckoning to be a very promising approach for determination of animal movements, for elucidating habitat preferences and, with its high spatial and temporal resolution, a powerful methodology for highlighting particular movement patterns that are indicative of behavioural processes (Viswanathan et al., 1996, 1999; Frair et al., 2005; Benhamou, 2004) (such as specific tracks resulting from tracking prey via scent). Our ability to recognise these latter elements, however, necessitates an analytically robust approach so that the behavioural elements in movement become apparent irrespective of the scale over which they

occur. This is where the proposed AII analysis could play a useful role.

#### 4.3. Value of AII analysis

The primary value in AII data, and particularly in the contour plots presented here, is that the multi-scale tortuosity of complete animal tracks can be immediately visually assessed without bias for scale. In addition, representation of this tortuosity over time means that temporal changes in the convolutions of tracks are also apparent, although if long periods are graphed out small events tend to become lost (cf. Fig. 5). Although not considered statistically, our data show striking interspecific differences in AII contour plots, which presumably reflect search strategies for the animals concerned. These



strategies are primarily defined by the extent of straight-line travel in the plots (white surfaces) and the degree to which it is broken up by convolution events (the shaded surfaces) with more tortuosity (Benhamou, 2004) (Fig. 4). Although in this work, we simply qualitatively describe features of the AII contour plots, the form of convolution events could be described mathematically so that particular shapes could be assessed for their degree of incidence and clustering. Matrices of convolution events could be built up incorporating; the shape of particular contour intervals (Gielis, 2003), the integral of the convolution event, the scale over which it occurred, and its temporal proximity to other convolution events. In addition, where convolution events are determined (by some statistically objective process) to be vertical bars (cf. Fig. 4) the width of the bar, the position of its AII peak and the rate of decrease of its value across the scale also could describe the convolution event. Mathematical descriptions of convolution events would mean that they could be examined for clustering with a view to identifying particular types of movement indicative of some specific process. Since the data used also give animal position, then the occurrence of particular processes can be ascribed to locations and consideration given to the adaptive significance of that behaviour at the specific place. Overall, since most of our equipped animals were foraging, convolution events are likely to be associated with one of three major processes—(a) simple search for prey without reference to a cue, (b) search for prey following a cue, or (c) prey acquisition following, e.g., pursuit. We suggest that detailed description of the apparent convolution events might reveal species-specific patterns that represent foraging strategies. For example, an expected convolution event for an animal honing in on prey by scent would be a bar slanting from the top left to the bottom right (Fig. 9A) while an animal gradually expanding the area of search having previously discovered prey (an appropriate strategy in an area where prey tend to be clumped) would be a vertical mirror image of this (Fig. 9B). A combination of the two processes should create a V-shape (Fig. 9C) though we have, as yet, not observed this pattern in our data.

Convolution events at very fine scales also can represent characteristic patterns resulting from the biomechanics of movement. For example, the typical patterns of movement of procellariiformes during dynamic soaring (Walker and Westneat,

2000; Stocker and Weihs, 1998; Bishop, 2005) may, depending on wind and wave conditions, result in a characteristic wave pattern in horizontal movement (Fig. 5), which appears on the AII contour plot as a series of similar repeating convolution events (Fig. 5—highlighted section A). It is notable here that our data from the wandering albatross indicate that during flight this bird did not have an AII of greater than 0.1 at intervals of less than about 4 s. At flight speeds of ca. 20 m/s (H. Weimerskirch, Unpubl. data) the bird covered 80 m in 4 s over and had an effective minimum flight circle radius of over 350 m. In this case, the fact that our AII contour plot effectively shows no convolution events at scales of less than 4 s demonstrates that, during flight at least, this data set achieves minimum resolution desirability for determining animal movement. Since wandering albatrosses cannot turn more tightly during flight than that calculated, it means that with the current resolution we are able to detect any movement pattern that the bird might initiate. Clearly though, similar studies for penguins, with their remarkable manoeuvrability (Hui, 1985) would require sub-second sampling frequencies. We suggest that, where possible, it is desirable for the sampling frequency of dead-reckoning or GPS systems to be set so that the minimum turn radius of the animal in question is reflected in convolution events that do not meet the point where the scale axis crosses the time axis in the AII contour plot (cf. Fig. 4 Adelle with Fig. 5C).

Most of our examples of AII contour plots deal with changes in two dimensions in the horizontal plane but the process also can be carried out in three dimensions or two dimensions in the vertical plane. This is particularly relevant for animals such as fish that are not constrained to return to the sea surface in order to breathe. Diving species that breathe air must always return to the sea surface and thus, in a three-dimensional AII contour plot, they would tend to have regular convolution events that correspond to this. This is a demonstration of how the AII methodology highlights particular behavioural events, in this case the dive. Depending on the question asked, however, it may be more relevant to examine movement with emphasis on changes in vertical movement so that a two-dimensional AII can be constructed where one dimension is depth. It is even feasible to present an AII contour plot for a single dimension although, understandably, this is most useful for species that

do not repeatedly and rapidly move up and down an appreciable part of the water column.

Finally, for many animals that travel at constant speed (Hui, 1983, 1987, 1988), the AII contour plots with  $x$ - and/or  $y$ -axes as time can be easily converted to distance (one or both). This has the advantage of giving the worker a good idea of the spatial scale over which the convolution events occur. Where swim speed is not constant, the conversion is more problematic, and where different travel modes incorporate very different speeds, such as in the case of the Imperial Cormorant flying or swimming, small-scale tortuosity in the low-speed mode may be hidden in the large amount of the plot consecrated to high-speed travel.

Animal movements and behaviour are tremendously complex although patterns are now becoming increasingly apparent (Viswanathan et al., 1996) and the potential benefits to the animals engaged in these behaviours are also becoming more transparent (Viswanathan et al., 1999). Our abilities to test predictions about how animals move and behave depend, however, primarily on our capacity to document what is happening. This documentation necessitates systems for measuring what actually happens in the field as well as analytical methods. With the huge advances in solid-state electronics, dead-reckoning is now a real alternative to other position determining systems and at times is the only option. This, coupled with the formulation for AIIs with the derived contour plots, promises to be a useful tool in the attempt to understand the patterns that animals display in their movements as well as the reasons behind them.

### Acknowledgements

The work on sea lions was supported by the Deutsche Forschungsgemeinschaft (Wi 1023/10-1) and the Wildlife Conservation Society. The help of M. Uhart, B. Raphael, P. Calle and D.A. Albareda with the anaesthesia of the sea lions, and of V. Ramos and P. Ledesma in recovering the dead-reckoners is gratefully acknowledged. Permission to carry out the work was granted by the Dirección de Fauna and Subsecretaría de Turismo de la Provincia del Chubut, Argentina. The study on porpoises was co-sponsored by the “Deutsche Umwelthilfe e.V.”, Radolfzell, Germany. We thank the pound net fishermen from Korsør, Gunnar Nielsen and Tage Mortensen, who provided the live harbour porpoise. We also wish to thank Genevieve

Desportes for help during the tagging, Finn Larsen for attempts in recovering the tag and Antje Steinfurth for help with the analysis. Gunther Dorn, Uwe Lenz and Mandy Kierspel helped with the device construction. We thank Lee Miller for valuable criticism of the paper. The study was carried out under the Danish permission from Skovog Naturstyrelsen (Danish Forest and Nature Agency, SN 343/SN-0008) and Dyreforsøgstilsynet (animal experiment inspection, 1995-101-62), the experiments comply with the current laws in Denmark. We are grateful to two referees for their insights and helpful criticism.

### References

- Anderson, C.R., Lindzey, F.G., 2003. Estimating cougar predation rates from GPS location clusters. *Journal of Wildlife Management* 67, 307–316.
- Bannasch, R., Wilson, R.P., Culik, B., 1994. Hydrodynamic aspects of design and attachment of a back-mounted device in penguins. *Journal of Experimental Biology* 194, 83–96.
- Benhamou, S., 2004. How to reliably estimate the tortuosity of an animal's path: straightness, sinuosity, or fractal dimension? *Journal of Theoretical Biology* 229, 209–220.
- Bishop, C.A., 2005. Circulatory variables and the flight performance of birds. *Journal of Experimental Biology* 208, 1695–1708.
- Blackwell, S.B., Haverl, C.A., Le Boeuf, B.J., Costa, D.P., 1999. A method for calibrating swim-speed recorders. *Marine Mammal Science* 15, 894–905.
- Block, B.A., Dewar, H., Blackwell, S.B., Williams, T.D., Prince, E.D., Farwell, C.J., Boustany, A., Teo, S.L.H., Seitz, A., Walli, A., Fudge, D., 2001. Migratory movements, depth preferences, and thermal biology of Atlantic bluefin tuna. *Science* 293, 1310–1314.
- Bradshaw, C.J.A., Hindell, M.A., Sumner, M.D., Michael, K., 2004. Loyalty pays: potential life history consequences of fidelity to marine foraging regions by southern elephant seals. *Animal Behaviour* 68, 1349–1360.
- Carpenter, P.W., Davies, C., Lucey, A.D., 2000. Hydrodynamics and compliant walls: does the dolphin have a secret? *Current Science* 79, 758–765.
- Dallantonia, L., Dallantonia, P., Benvenuti, S., Ioale, P., Massa, B., Bonadonna, F., 1995. The homing behavior of Cory's shearwaters (*Calonectris diomedea*) studied by means of a direction recorder. *Journal of Experimental Biology* 198, 359–362.
- Davis, R.W., Fuiman, L.A., Williams, T.M., Collier, S.O., Hagey, W.P., Kanatous, S.B., Kohin, S., Horning, M., 1999. Hunting behaviour of a marine mammal beneath the Antarctic fast ice. *Science* 283, 993–996.
- Eckert, S.A., 2002. Swim speed and movement patterns of gravid leatherback sea turtles (*Dermochelys coriacea*) at St Croix, US Virgin Islands. *Journal of Experimental Biology* 205, 3689–3697.
- Fedak, M.A., 2004. Marine animals as platforms for oceanographic sampling: a “win/win” situation for biology and

- operational oceanography. *Memoirs of the National Institute for Polar Research* 58, 133–147.
- Ferraroli, S., Georges, J.Y., Gaspar, P., Le Maho, Y., 2004. Where leatherback turtles meet fisheries. *Nature* 429, 521–522.
- Frair, J.L., Nielsen, S.E., Merrill, E.H., Lele, S.R., Boyce, M.S., Munro, R.H.M., Stenhouse, G.B., Beyer, H.L., 2004. Removing GPS collar bias in habitat selection studies. *Journal of Applied Ecology* 41, 201–212.
- Frair, J.L., Merrill, E.H., Visscher, D.R., Fortin, D., Beyer, H.L., Morales, J.M., 2005. Scales of movement by elk (*Cervus elaphus*) in response to heterogeneity in forage resources and predation risk. *Landscape Ecology* 20, 273–287.
- Fritz, H., Said, S., Weimerskirch, H., 2003. Scale-dependent hierarchical adjustments of movement patterns in a long-range foraging seabird. *Proceedings of the Royal Society of London Series B: Biological Sciences* 270, 1143–1148.
- Gielis, J., 2003. A generic geometric transformation that unifies a wide range of natural and abstract shapes. *American Journal of Botany* 90, 333–338.
- Hays, G.C., Houghton, J.D.R., Myers, A.E., 2004a. Pan-Atlantic leatherback turtle movements. *Nature* 429, 522.
- Hays, G.C., Metcalfe, J.D., Warne, A.W., 2004b. The implications of lung-regulated buoyancy control for dive depth and dive duration. *Ecology* 85, 1137–1145.
- Hill, R.D., 1994. Theory of geolocation by light levels. In: LeBoeuf, B.J., Laws, R.M. (Eds.), *Elephant Seals: Population Ecology, Behaviour, and Physiology*. University of California Press, Berkeley, CA, pp. 227–236.
- Hindell, M.A., Harcourt, R., Waas, J.R., Thompson, D., 2002. Fine-scale three-dimensional spatial use by diving, lactating female Weddell seals *Leptonychotes weddellii*. *Marine Ecology Progress Series* 242, 275–284.
- Hochscheid, S., Wilson, R.P., 1999. A new method for the determination of at-sea activity in sea turtles. *Marine Ecology Progress Series* 185, 293–296.
- Hooker, S.K., Whitehead, H., Gowans, S., Baird, R.W., 2002. Fluctuations in distribution and patterns of individual range use of northern bottlenose whales. *Marine Ecology Progress Series* 225, 287–297.
- Hui, C.A., 1983. Energetics of penguin swimming. *American Zoologist* 23, 956.
- Hui, C.A., 1985. Maneuverability of the Humboldt penguin (*Spheniscus humboldti*) during swimming. *Canadian Journal of Zoology* 63, 2165–2167.
- Hui, C.A., 1987. The porpoising of penguins—an energy-conserving behavior for respiratory ventilation. *Canadian Journal of Zoology* 65, 209–211.
- Hui, C.A., 1988. Penguin swimming. II: energetics and behavior. *Physiological Zoology* 61, 344–350.
- Johnson, M.P., Tyack, P.L., 2003. A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *IEEE Journal of Oceanic Engineering* 28, 3–12.
- Jouventin, P., Weimerskirch, H., 1990. Satellite tracking of Wandering albatrosses. *Nature* 343, 746–748.
- Kooyman, G.L., 2004. Genesis and evolution of bio-logging devices: 1963–2002. *Memoirs of the National Institute for Polar Research* 58, 15–22.
- Kreye, J., 2003. Messung der Schwimmgeschwindigkeit und deren Konsequenzen für luftatmende marine Vertebraten am Beispiel des Magellanpinguins (*Spheniscus magellanicus*). M.Sc. thesis, Zoologisches Institut, Naturwissenschaftlich-Technische Fakultät III. Universität des Saarlandes, Saarbrücken, p. 121.
- Mitani, Y., Sato, K., Ito, S., Cameron, M.F., Siniff, D.B., Naito, Y., 2003. A method for reconstructing three-dimensional dive profiles of marine mammals using geomagnetic intensity data: results from two lactating Weddell seals. *Polar Biology* 26, 311–317.
- Ponganis, P.J., Kooyman, G.L., Zornow, M.H., Castellini, M.A., Croll, D.A., 1990. Cardiac output and stroke volume in swimming harbour seals. *Journal of Comparative Physiology* 160B, 473–482.
- Ropert-Coudert, Y., Kato, A., Sato, K., Naito, Y., Baudat, J., Bost, C.A., Le Maho, Y., 2002. Swim speed of free-ranging Adelia penguins *Pygoscelis adeliae* and its relation to the maximum depth of dives. *Journal of Avian Biology* 33, 94–99.
- Sato, K., Mitani, Y., Cameron, M.F., Siniff, D.B., Naito, Y., 2003. Factors affecting stroking patterns and body angle in diving Weddell seals under natural conditions. *Journal of Experimental Biology* 206, 1461–1470.
- Sims, D.W., Southall, E.J., Tarling, G.A., Metcalfe, J.D., 2005. Habitat-specific normal and reverse diel vertical migration in the plankton-feeding basking shark. *Journal of Animal Ecology* 74, 755–761.
- Springer, B., 1992. Das problem der bestimmung von Bewegungsaktivitäten bei warmblütigen Tieren. M.Sc. thesis, University of Kiel, Kiel, pp. 91.
- Stocker, S., Weihs, D., 1998. Bird migration—an energy-based analysis of costs and benefits. *IMA Journal of Mathematics Applied in Medicine and Biology* 15, 65–85.
- Sundstrom, L.F., Gruber, S.H., 1998. Using speed-sensing transmitters to construct a bioenergetics model for subadult lemon sharks, *Negaprion brevirostris* (Poey), in the field. *Hydrobiologia* 372, 241–247.
- Viswanathan, G.M., Afanasyev, V., Buldyrev, S.V., Murphy, E.J., Prince, P.A., Stanley, H.E., 1996. Levy flight search patterns of wandering albatrosses. *Nature* 381, 413–415.
- Viswanathan, G.M., Buldyrev, S.V., Havlin, S., da Luz, M.G.E., Raposo, E.P., Stanley, H.E., 1999. Optimizing the success of random searches. *Nature* 401, 911–914.
- Walker, J.A., Westneat, M.W., 2000. Mechanical performance of aquatic rowing and flying. *Proceedings of the Royal Society of London Series B: Biological Sciences* 267, 1875–1881.
- Weimerskirch, H., Le Corre, M., Jaquemet, S., Marsac, F., 2005. Foraging strategy of a tropical seabird, the red-footed booby, in a dynamic marine environment. *Marine Ecology Progress Series* 288, 251–261.
- Wilson, R.P., Liebsch, N., 2003. Up-beat motion in swinging limbs: new insights into assessing movement in free-living aquatic vertebrates. *Marine Biology* 142, 537–547.
- Wilson, R.P., Wilson, M.P., 1988. Dead reckoning—a new technique for determining penguin movements at sea. *Meeresforschung—Reports on Marine Research* 32, 155–158.
- Wilson, R.P., Puetz, K., Bost, C.A., Culik, B.M., Bannasch, R., Reins, T., Adelung, D., 1993. Diel dive depth in penguins in relation to diel vertical migration of prey—whose dinner by candlelight. *Marine Ecology Progress Series* 94, 101–104.
- Wilson, R.P., Culik, B.M., Bannasch, R., Lage, J., 1994. Monitoring Antarctic environmental variables using penguins. *Marine Ecology Progress Series* 106, 199–202.
- Wilson, R.P., Grémillet, D., Syder, J., Kierspel, M.A.M., Garthe, S., Weimerskirch, H., Schäfer-Neth, C., Alejandro Scolaro, J., Bost, C.-A., Plötz, J., Nel, D., 2002a. Remote-sensing systems

- and seabirds: their use, abuse and potential for measuring marine environmental variables. *Marine Ecology Progress Series* 228, 241–261.
- Wilson, R.P., Ropert-Coudert, Y., Kato, A., 2002b. Rush and grab strategies in foraging marine endotherms: the case for haste in penguins. *Animal Behaviour* 63, 85–95.
- Wilson, R.P., Kreye, J.A., Lucke, K., Urquhart, H., 2004. Antennae on transmitters on penguins: balancing energy budgets on the high wire. *Journal of Experimental Biology* 207, 2649–2662.
- Yoda, K., Naito, Y., Sato, K., Takahashi, A., Nishikawa, J., Ropert-Coudert, Y., Kurita, M., Le Maho, Y., 2001. A new technique for monitoring the behaviour of free-ranging Adelie penguins. *Journal of Experimental Biology* 204, 685–690.
- Zimmer, W.M.X., Madsen, P.T., Teloni, V., Johnson, M.P., Tyack, P.L., 2005. Off-axis effects on the multipulse structure of sperm whale usual clicks with implications for sound production. *Journal of the Acoustical Society of America* 118, 3337–3345.