Identifying Leatherback Turtle Foraging Behaviour from Satellite Telemetry Using a Switching State-Space Model

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Running Headline: Identifying Leatherback Foraging Behaviour

Abstract

Identifying foraging habitat of marine predators is vital to understanding the ecology of these species and for their management and conservation. Foraging habitat for many marine predators is dynamic and this poses a serious challenge for understanding how oceanographic features may shape the ecology of these animals. To help resolve this issue, we present a switching state-space model (SSSM) for discerning different movement behaviours hidden within error-prone satellite telemetry data. Along with modelling the movement dynamics, the SSSM estimates the probability that an animal is in a particular discrete behavioural mode, such as transitting or foraging. Using Argos satellite telemetry for leatherback sea turtles we show that the SSSM readily identifies distinct classes of movement behaviour from the noisy data. Moreover, patterns in simultaneously collected diving data, to which the model is blind, match well with behavioural mode estimates. By combining behavioural mode estimates from the model with the diving data we show that while transitting, leatherbacks make longer, deeper dives, and while foraging, they encounter cooler waters that range from 13-22 °C. These differences are consistent among the turtles studied and within the same turtle in different years. This modelling approach can enhance standard kernel density estimators for identifying habitat use by incorporating behavioural information into the estimation procedure. Ultimately, we can build predictive models of habitat use by incorporating environmental data and diving behaviour directly into the SSSM framework.

Keywords

Bayesian, *Correlated random walk*, *Dermochelys coriacea*, *Diving behaviour*, *Habitat*, *Hidden Markov Models*, *Meta-Analysis*, *Uncertainty*

INTRODUCTION

Electronic tracking of marine predators has revealed a wealth of information on patterns of distribution and habitat use (Block *et al.*, 2005), migratory patterns (Block *et al.*, 2001), and foraging ecology (Sale *et al.*, 2006). We contend, however, that even more information can be extracted from these data by applying modern statistical methods that deal with both biological and statistical complexity in the data (Jonsen *et al.*, 2005; Nielsen *et al.*, 2006) and that allow estimation of hidden processes that are intractible to other approaches.

Several approaches have been developed recently that allow estimation of hidden states from time series data. State-space models have great potential for modelling population times series data and have been generalized to admit a variety of population data types and analyses (Newman *et al.*, 2006). The state-space approach also was proposed as a powerful tool for modelling animal movement data because of its ability to deal simultaneously with potentially large measurement errors and variability in the dynamics of movement (Jonsen *et al.*, 2003). Hidden Markov models, unlike state-space models, do not estimate dynamics, but they can identify hidden patterns in the data and this is essentially the approach used by Morales *et al.* (2004). They analysed GPS telemetry on elk movements and showed how a switching model could be used to reveal long- and short-range movement behaviours hidden in the data. Jonsen *et al.* (2005) further developed the switching idea by showing how different behaviours that were obscurred by measurement error in Argos satellite telemetry data could be estimated using a state-space approach that modelled the movement dynamics and accounted for uncertainty in both the observations and the dynamics. The fundamental advantage of the state-space approach is that movement dynamics are modelled explicitly and this allows more complex behaviour to be captured, even when the issue of measurement error is minor such as with GPS data.

Here we consider the application of a switching state-space model (SSSM) to the issue of identifying foraging behaviour from remotely sensed tracking data, a situation where direct observation is not possible. When animals encouter areas of sufficiently abundant prey, they often engage in area-restricted search by decreasing their travel rate and/or increasing their turning frequency and angle (Turchin, 1991). Conversely, animals encountering unsuitable habitat often have fast travel rates and infrequent and small turning angles (Turchin, 1991). These differences in movement behaviour can form the basis for estimating nominal foraging and transitting behaviours from a time series of observed positions. To identify different behaviours that may be hidden in the position data, we employ an SSSM. The purpose of an SSSM is to estimate: (1) unobservable "true" positions, termed state estimates, (2) movement parameters from a specifed process model, and (3) hidden behavioural states from data observed with error. Hereafter we refer to these behavioural states as behavioural *modes* to avoid confusion with the state estimates.

We illustrate our approach by fitting an SSSM to Argos-derived positions of leatherback turtles off the coasts of eastern Canada and the northeastern US. The leatherback turtle, *Dermochelys coriacea*, is a cosmopolitan marine species that undertakes a variety of migratory patterns (Luschi *et al.*, 2003; James *et al.*, 2005a). Leatherbacks tagged off Nova Scotia, Canada, make annual return migrations from tropical to sub-Arctic waters (James *et al.*, 2005a) with much of their time in northern waters presumably spent foraging on gelatinous zooplankton (James *et al.*, 2006a). Despite a growing awareness of the migratory strategies and behaviours (James *et al.*, 2005a; Jonsen *et al.*, 2006) and population characteristics

(James *et al.*, in press) of these animals, we know remarkably little about how these animals utilize foraging habitat and even less about the ecology of their jellyfish prey (Witt *et al.*, in press). Efforts to identify habitats important to this species (James *et al.*, 2005b) are urgently needed given its critically endangered status (IUCN, 2004). To this end we illustrate how SSSM's can be used to estimate locations where turtles are foraging based solely on the information contained in the time series of their observed positions. Then, as a means of corroborating the SSSM predictions, we compare estimated switches between behavioural modes to observed changes in patterns of diving activity which were collected simultaneously. Finally, using all the suitable telemetry data available to us, we describe differences in diving behaviour and the thermal enivronment of leatherback turtles that engage in foraging versus transitting behaviours.

MATERIALS AND METHODS

Data

The data consist of Argos-derived surface positions obtained from satellite-linked time-depth recorders (SLTDRs; model SSC3, Wildlife Computers, Redmond, WA, USA) attached to leatherback turtles captured in waters off Nova Scotia, Canada (see James *et al.*, 2005b, for details). We focus our analyses on movement behaviours and diving data in the northeastern Atlantic ($> 36°$ N) off of eastern North America where the turtles spend considerable time foraging (James *et al.*, 2005b).

In addition to providing surface positions, the SLTDRs collect and relay data on time at depth, time at temperature, maximum dive depth and dive duration. These dive data are not directly associated with the recorded positions rather they are binned within 14 user-defined data ranges over 6-hr collection periods. Periods were set such that one consistently encompassed night and one encompassed day (Night: 2100-0300; Morning: 0300-0900; Day: 0900-1500; Evening: 1500-2100; Atlantic Daylight Time). Time at depth and time at temperature reflected all time when SLTDRs were submerged, whereas dives were registered only when turtles descended below 4 m or 6 m. These data are transmitted in histogram format to increase ease of transfer via the limited bandwidth of the Argos satellite system. Nonetheless, patterns in diving behaviour can be readily identified and compared with the behavioural estimates from the SSSM described below.

Suitable data were available for five turtles, two of which were deployed with tags set to record continuously and three with tags that were duty-cycled (set to record every second 24 h period). Leatherbacks in these northern waters complete annual return migrations from tropical waters in the Carribean or South America (James *et al.*, 2005a) and four of the five tags (3 duty-cycled, 1 continuously recording) transmitted long enough to record parts of two successive seasons spent foraging in northern waters. We consider only those portions of the data North of 35 ° Lat where the turtles appear to forage extensively. The duration of observed tracks ranged from 49 to 216 d (mean 124 d ± 46 sd).

The switching state-space model

Here we describe the components of the SSSM employed to estimate hidden behavioural modes, states, and movement parameters from Argos satellite telemetry data.

We use a first-difference correlated random walk model (DCRW) (Jonsen *et al.*, 2005) to model the movement process. The DCRW assumes a correlated random walk on the differences in successive locations, not on the locations themselves. This makes sense intuitively as the behaviour we are interested in is how animals change their speed and direction, not how they change their location per se. Written as a state-space process model in 2 dimensions, the DCRW has the following form,

$$\mathbf{d}_t \sim N_2(\gamma \mathbf{T}(\theta)\mathbf{d}_{t-1}, \mathbf{\Sigma}). \tag{1}$$

where $\mathbf{d}_{t-1}$ is the difference between the locations $\mathbf{x}_{t-1}$ and $\mathbf{x}_{t-2}$, and $\mathbf{d}_t$ is the difference between the locations $\mathbf{x}_t$ and $\mathbf{x}_{t-1}$. $\mathbf{T}(\theta)$ is a transition matrix that provides the rotation required to move from $\mathbf{d}_{t-1}$ to $\mathbf{d}_t$, where θ is the mean turning angle. N_2 is a bivariate Gaussian distribution with covariance matrix $\mathbf{\Sigma}$. We include γ to allow for variability in the autocorrelation of direction and speed; with $\gamma = 0$ resulting in a simple random walk and $0 < \gamma < 1$ yielding a random walk with correlation in both direction and move speed.

The second component of the state-space model relates the unobserved states predicted by the process model to the observed data, consequently it is termed the observation model. Rather than use a simple model where each unobserved state corresponds to an observed location, we must account for the irregular sampling of positions, the variable quality of Argos observations, and their non-Gaussian errors (see Jonsen *et al.*, 2005, for full details).

We let i be an index for locations (if any are observed) between time t and $t+1$, i.e. $i = (0, \ldots, n_t)$. We make the simplifying assumption that animals travel in a straight line between $\mathbf{x}_{t-1}$ and $\mathbf{x}_t$. This poses no difficulty for state transitions with reasonably short time steps, relative to the resolution of the data,

$$\mathbf{y}_{t,i} = (1 - j_i)\mathbf{x}_{t-1} + j_i\mathbf{x}_t + \boldsymbol{\epsilon}_t \tag{2}$$

where $\mathbf{y}_{t,i}$ is the ith observed position during the regular time interval $t-1$ to t, j_i is the proportion of this time interval at which the ith observation is made ($0 < j_i < 1$), and $\boldsymbol{\epsilon}_t$ is a random variable representing the error in the Argos-derived positions. Note that the j_i's can be calculated from the data if the time of day is recorded with each observed location and that for regular time intervals where no observations exist, we set $i = 1$ and $j_i = 0.5$. Because Argos position errors can be strongly non-Gaussian (Jonsen *et al.*, 2005), we model the errors with generalized t-distributions which are robust to extreme values. In addition, Argos categorizes positions into 6 quality classes and we use this information to determine the appropriate t-distribution parameters to use for each position in the observation model. For estimation errors in latitude or longitude of quality class q ($q = 1, \ldots, 6$) we let $\boldsymbol{\epsilon}_{q(i),t} \sim t(0, \boldsymbol{\tau}_{q(i),t}, \boldsymbol{\nu}_{q(i),t})$, where $\boldsymbol{\tau}_{q(i),t}$ is the scale parameter and $\boldsymbol{\nu}_{q(i),t}$ is the degrees of freedom. When fitting the state-space model to the Argos-derived position data we fix the $\boldsymbol{\epsilon}_t$'s to values estimated from independent data (Jonsen *et al.*, 2005), thereby avoiding the need to estimate an additional 24 parameters.

With the state-space model described above we can estimate the unobserved states $\mathbf{x}_t$ and the parameters of the DCRW model, θ, γ and $\boldsymbol{\Sigma}$. We still require a method to identify discrete behavioural modes from the position data. To do this we specify a process model for each behavioural mode we believe exists in the data, i.e. we use an index b_t to denote behavioural mode on the parameters, θ and γ (Morales *et al.*, 2004). Thus Eq. 1 becomes:

$$\mathbf{d}_t \sim N_2(\gamma_{b_t}\mathbf{T}(\theta_{b_t})\mathbf{d}_{t-1}, \mathbf{\Sigma}), \tag{3}$$

where $b_t = k, k \in \{1, \ldots, B\}$ and B is the total number of behavioural modes to be estimated. Here we consider two general behaviours, nominally, transitting and foraging. This is the DCRWS model (from Jonsen *et al.*, 2005).

The analysis now involves the estimation of two sets of unobserved variables, the $\mathbf{x}_t$'s and the b_t's, and the estimation of the parameters θ, γ, and $\mathbf{\Sigma}$. We can estimate the b_t's using a mixture model approach, which assumes that what an animal is doing now is independent of what it was doing previously. However, a more realistic approach is to assume that what an animal is doing now depends to some extent upon what it was doing previously. With this in mind, we make use of a switching model (Morales *et al.*, 2004; Jonsen *et al.*, 2005) where the movement parameters θ and γ are indexed by behavioural mode. In our case we are interested in transitting and foraging behaviours, so there are four possible transitions and we must estimate two of these. We let α_1 be the probability of an animal transitting at time t given it was also transitting at time $t-1$ and we let α_2 be the probability of an animal transitting at time t given it was foraging at time $t-1$.

We use a Bayesian approach to fit the model, placing vague priors on model parameters (see Jonsen *et al.*, 2005, for details), except for the movement parameters for the transitting mode; θ_1 and γ_1. For these parameters we used the following priors, $\theta_1 \sim Beta(20, 20)$ and $\gamma_1 \sim Beta(48, 16)$, reasoning that while transitting, turn angles should be closer to 0 and autocorrelation should be higher than when foraging. The model was fit with the freely available WinBUGS software (Spiegelhalter *et al.*, 2004) which uses Markov Chain

Monte Carlo (MCMC) methods to approximate the multi-dimensional integration required in Bayesian analyses. The model was fit to each dataset with a total of 30 000 MCMC samples, the first 10 000 were discarded as a burn-in and the remaining 20 000 samples were thinned out to 4 000 samples by retaining only every 5th sample to reduce autocorrelation. Parameter, state, and behavioural mode estimates were based on these final 4 000 samples. Model code is provided in Supplement 1.

Analyses

We used the diving statistics described earlier, which show relatively clear behavioural patterns (James *et al.*, 2006a), as a means of corroborating the estimates of b_t obtained from the DCRWS model. Because b_t is a discrete parameter, values can only be 1 or 2, we used the means of the MCMC samples as a convenient way to visualize behavioural switches. We, therefore, delineated the two behavioural modes by adopting cutoffs at 1.25 and 1.75; mean estimates below 1.25 were considered to represent transitting and mean estimates above 1.75 were considered to represent foraging. Mean estimates between 1.25 and 1.75 were treated as uncertain, ie. there was insufficient information to distinguish between the behaviours in these cases. We view this as a conservative approach to classifying the behaviour modes as one could easily assume a single cutoff of 1.5.

We used a graphical approach, overlaying a time series histogram of binned diving statistics (14 data ranges in 6-hr collection intervals) with b_t (also at 6-hr intervals) to look for congruence between estimated switches in b_t and obvious changes in the temporal pattern of the diving statistics. We also aggregated the data over time and compared the proportion of dives that occured while turtles were predicted to be transitting or foraging within each of the 14 data ranges. Finally, for each diving statistic we present plots of the difference in the mean for time periods when the turtle was transitting versus foraging. The means of the diving statistics were calculated from time series data and we accounted for autocorrelation by estimating the effective sample size (Bayley & Hammersley, 1946) and adjusting the df for the confidence intervals. The differences between transitting versus foraging for temperature, time at depth, dive duration and maximum dive depth were each combined using a random effects meta-analysis (Worm & Myers, 2003). As mentioned earlier, four of the tags provided data on successive foraging seasons in northern waters. We consider these multiple foraging seasons to be distinct enough to consider them as independent datasets in this analysis. We do, however, evaluate the more conservative assumption of non-independence among tracks from the same turtle.

RESULTS

Maps of state estimates with associated behavioural modes (Fig. 1 and Fig. S2-1) indicate that two of turtles spent a considerable proportion of time (0.74, turtle A; 0.55, turtle B.1) foraging in shelf (Fig. 1, red circles) or slope (Fig. S2-1, red circles) waters off Canada and the northeastern United States. Estimated foraging bouts for the other turtles occurred in waters from 37 to 50 °N with most bouts occurring in slope waters south and east of George's Bank, the southern Gulf of St. Lawrence, and off northeastern Cape Breton Island. The proportion of time spent foraging in northern waters by these turtles ranged from 0.28 to 0.76.

There was relatively little uncertainty in the behavioural mode, as less than 10 % of state estimates had behavioural modes estimated between 1.25 and 1.75 (Fig. 1, black circles). These uncertain behavioural modes were associated either with short transition periods from transitting to foraging (or vice-versa) or with short intervals (i.e., 12 - 18 h) of faster, directed movement embedded within longer foraging bouts. The latter may suggest either the presence of a third behavioural mode or an inability of the model to estimate switches from foraging to transitting back to foraging over such a short time interval. Use of a time step shorter than 6 h might yield better behavioural mode estimation in these instances but this may come at the cost of overly conservative estimation of foraging modes due to the scale-dependent nature of the θ and γ parameters.

Marginal posterior distributions of the parameters θ_k and γ_k showed no overlap between the two behavioural modes, suggesting that the modes indeed represent distinct classes of movement (Table S2-1). As would be expected for transitting animals, the median θ_1 is near 0 and the median γ_1 is relatively high (see Fig. S2-2 for examples). Foraging animals typically exhibited some form of area-restricted search with large turning angles and relatively slow travel rates (e.g., Fig. 1, red circles). The median θ_2's indicate that turtles tend to reverse their direction frequently (at a 6-h time scale) while foraging (Table S2-1). The turtles also showed relatively low autocorrelation in their turns and speed (Table S2-1), indicating a lack of persistence in turn angle and travel rate from one time step to the next. Travel rates calculated from the state estimates ($\mathbf{x}_t$) were also clearly distinguishable between the two behavioural modes (e.g., see Fig. S2-3).

The means of the estimated b_t's, which range between 1 ($1 \leq$ transitting < 1.25) and 2 ($1.75 <$ foraging ≤ 2), match well with the temporal histograms of the diving statistics.

There appears to be close correspondence between switches from one behavioural mode to the other and variation in time at temperature. Temperatures sampled by the turtles were more stable when the model predicted the turtle was foraging (e.g., turtle B, Fig. 2), suggesting that, at least in northern waters, they forage in a relatively narrow temperature range of approximately 13 to 22 °C (e.g., turtle B, Fig. 3). Dive durations followed a similar pattern, in that duration increased with increasing temperature when the model predicted turtle were transitting, but durations tended to have no obvious trend (Fig. 2) and were generally shorter when turtles were predicted to be foraging (Fig. 3). There was reasonable correspondence between changes in the pattern of time spent in deeper water and switches from one behavioural mode to the other. Turtles spent the majority of their time in the upper 65 m of the water column regardless of behaviour, however, deeper dives were more often associated with transitting behaviour (Fig. 3) but were occasionally observed when turtles were foraging (see Fig. S2-4). Maximum depths attained naturally followed a similar pattern (Figs. 2 & 3). Representative plots for turtle A and a turtle (E.1) with a duty-cycled tag are provided in Supplement 2.

Using behavioural mode estimates and diving data for turtles with duty cycled and continuously recording tags, we found clear differences in the means of time at depth, temperature, dive duration, and maximum depth when turtles are transitting versus foraging (Fig. 4). When transitting turtles on average were 32 m (± 3.2 se, 8 df) deeper (Fig. 4a), in water 1.4 °C (± 0.38 se, 8 df) warmer (Fig. 4b), had maximum dives 25.5 m (± 1.97 se, 8 df) deeper (Fig. 4c), and had dives 6.6 min (± 0.98 se, 8 df) longer (Fig. 4d) than when foraging. The random effects means are also significantly different from 0 under the assumption of a lack of independence among annual foraging bouts of single turtles.

DISCUSSION

Our state-space approach for identifying foraging sites relies on estimating unobserved behavioural modes by modelling the dynamics of the movement process directly. A key assumption of our approach is that, given sufficient time, animal movement pathways are an integration of more than one behavioural mode. The resulting dynamics, represented by the time-series of observed positions, can be inherently nonlinear and are therefore best analysed with some form of switching model (Morales *et al.*, 2004; Jonsen *et al.*, 2005). SSSMs allow dynamics to be broken into discrete behavioural modes by specifying a process model for each behaviour and then estimating the probability of switching from one behavioural mode to another at each time step. In our case the process models for the transitting and foraging behaviours are functionally identical and differ only in the parameter values. This approach also allows for additional complexity such as modelling switches between more than two behaviours and modelling the influence of environmental features (Morales *et al.*, 2004) or physiological constraints on switching probabilities.

Search theory predicts that animals will change their behaviour and, consequently, their movement pattern as they encounter changes in habitat or prey density (Turchin, 1991). Typically, animals encountering prey at a sufficiently high density will engage in area-restricted search behaviours that are distinct from transitting or migration behaviour. Examination of observed Argos locations shows that leatherbacks engage in both area-restricted search and transitting behaviours but clear, objective delineation of the change points between behaviours is challenging due to the measurement errors in the data. By fitting an SSSM to the two-dimensional position data we were able to extract the behavioural dynamics obscurred by measurement error in the positions. Even though considerable information contained in the third dimension was ignored, the correspondence between behavioural mode predictions and the diving data suggests that behavioural estimation based only on the two-dimensional position data sufficiently captures the behavioural dynamics. Nevertheless, information on diving behaviour could be incorporated into the SSSM to further refine estimation of behavioural switches and identification of foraging habitat.

Because leatherbacks forage throughout the epipelagic and into the mesopelagic zones on gelatinous zooplankton (James *et al.*, 2005a), we assumed that corresponding changes in horizontal behaviour would be apparent in the vertical movement. Indeed the turtles tend to spend more time at greater depths and dive durations are longer when transitting versus foraging. This pattern lends support to the idea that leatherbacks may make scouting dives while transitting as an efficient means for sampling prey density (James *et al.*, 2006a) and perhaps opportunistic foraging without greatly reducing travel rate. Moreover, the shallower dives associated with extended, and presumably more profitable, foraging suggest that the turtles focus on regions where prey are available at shallower strata perhaps to reduce the energetic demands of foraging at depth. The thermal habitat of these foraging areas is slightly cooler than that associated with waters through which the turtles transit. The cooler waters associated with leatherback foraging may result from thermocline and, perhaps, an associated halocline effect on jellyfish movements (Graham *et al.*, 2001). The narrow range of temperatures experienced while foraging (13 to 22 °C) corresponds well with the average SST (16.6 °C) associated with peak sightings of leatherbacks off of Nova Scotia (James *et al.*, 2006b). Furthermore, a lack of bi-modality in the range of temperatures experienced while foraging suggests that leatherbacks do not cross frontal boundaries frequently, at least in the northern waters considered here (Polovina *et al.*, 2004).

Leatherbacks found off of South Africa engage in horizontal movements similar to the foraging and transitting behaviours shown here, but their movements do not correspond to simultaneously collected diving data (Sale *et al.*, 2006). Leatherbacks in this area may be transported by the tremendosuly strong Agulhas current system (Luschi *et al.*, 2003) and putative switches between transitting and foraging behaviours may simply be the result of advection rather than active behaviour per se. In the presence of strong currents, our model might incorrectly classify the behaviours, particularly when apparent area-restricted search behaviour is due purely to advection. In these situations more detailed models that incorporate information on ocean currents (Gaspar *et al.*, 2006) will be required to reliably identify behavioural states by parsing realized movements into passive advection and active behavioural components.

The SSSM approach to identifying multiple behaviours in movement data is more powerful than descriptive methods such as nonlinear curve-fitting to the log-frequency of behavioural events (Sibly *et al.*, 1990), path tortuosity and/or scale-dependency measures (Johnson *et al.*, 2002), and first-passage time analysis (Fauchald & Tveraa, 2003) because it permits the formulation and fitting of mechanistic movement models to the data (Morales *et al.*, 2004). In general, we need models based upon clear statistical principles that allow estimation of the dynamical parameters that capture the essence of complex movement behaviour; descriptive methods cannot do this.

Hidden Markov models have recently been used to estimate movement parameters including the probability of switching between different behavioural states (Morales *et al.*, 2004). The Hidden Markov approach is conceptually similar to our SSSM approach with the following two albeit related differences. First, by fitting a switching model in a state-space context we are able to model the dynamics of the movement process directly (Jonsen *et al.*, 2005). Hidden Markov models do not estimate dynamics per se and thus may be unable to capture more complex behavioural processes. Second, observation errors can be accounted for in the Hidden Markov context (Morales *et al.*, 2004), but they cannot be separated from variability in the underlying process that is implicitly being modelled. This drawback of the Hidden Markov approach will likely lead to overestimation of the observation errors, or, if the errors are assumed to be known, may lead to biased movement parameter estimates.

Identification of habitat and habitat use for marine predators is of critical importance for effective conservation and management efforts. Assessment of habitat use is dominated by kernel density estimation methods (Seaman & Powell, 1996) which give each observed position equal weight and ignore underlying behavioural mechanisms that constrain animal movement to particular regions or habitats. Our method can be used to inform kernel density estimation with behavioural information either by considering only those state estimates associated with foraging or by weighting the estimation with the b_t estimates (e.g., mean of MCMC samples for each b_t) so that state estimates associated with transitting carry little or no weight. Of course, a more powerful method would be to model directly the relationship between habitat features, such as sea surface temperature or current vectors, and movement behaviour (Jonsen *et al.*, 2003; Morales *et al.*, 2004) to gain a mechanistic understanding of how the animals interact with their environment.

CONCLUSIONS

Using an SSSM that assumes a first-difference correlated random walk on positions in space and time, we show that distinct classes of movement behaviour can be readily estimated from error-prone Argos telemetry data. Moreover, the switches between behavioural modes correspond with marked changes in the patterns of time at depth, temperature at depth, and dive duration. The correspondence between the model predictions and the diving data is impressive because the SSSM only makes use of information contained in the time series of positions to estimate the behavioural modes; the model is ignorant of the diving data. Further refinement of the behavioural mode estimation is possible by allowing the model switching to depend on the diving behaviour and/or environmental variables.

The leatherback turtle is one of the most difficult animals to study when they are foraging, furthermore, its jellyfish prey are nearly transparent and are even more difficult to study (but see Witt *et al.*, in press). Thus, our approach provides insights that cannot be obtained from other methods, but it would be useful to verify the predictions of our models using other independent data, for example, from sensors that detect changes in stomach temperature, mouth opening, and/or animal-borne video cameras. However, these methods are difficult to use for long periods of time for an animal that cannot usually be recaptured like a leatherback turtle.

State-space methods represent a critical advancement in the analysis of electronic tracking data by accounting for uncertainty in the data and by directly modelling the dynamics of animal behaviour. For example, the uncertainty in Argos-derived positions can be an order of magnitude greater than the distances over which foraging animals typically move (Jonsen *et al.*, 2005). In these situations, use of standard methods such as travel rate filters to remove suspect observations will inevitably yield misleading results (Jonsen *et al.*, 2006). Only by explicitly accounting for uncertainty in the data and modelling the dynamic nature of behavioural processes can we gain meaningful insight into the interactions between animals and their environment.

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Figure Captions

Figure 1. State estimates ($\mathbf{x}_t$'s, filled circles) with associated behavioural mode estimates (blue = transitting, red = foraging, black = uncertain) obtained from the SSSM for a leatherback turtle (B.1) tagged in coastal waters off Nova Scotia, Canada. The full path is shown inset. The underlying grey line indicates the observed Argos positions. The time interval between the $\mathbf{x}_t$'s is 6 h. The 1000 m isobath is displayed as a dashed black line.

Figure 2. Temporal histograms of time at depth, dive duration, water temperature, and maximum dive depth for turtle B.1 (non-duty-cycled tag). The bins presented on the left vertical axis are the 14 user-defined ranges for each variable. The coloured shingle in each bin indicates percentage of time or dives observed in that range over a 6-hour period. The time periods are: 2100 - 0300; 0300 - 0900; 0900 - 1500; 1500 - 2100 hours. The labels indicate the mid-point of each bin. Bins shaded grey indicate no dives were observed in that range for that 6-hr time period. Estimated behavioural mode b_t for each 6-hr period is overlaid (solid black line). Estimates less than 1.25 (lower dashed line) represent transitting (blue circles in Fig. 1), estimates greater then 1.75 (upper dashed line) represent foraging (red circles in Fig. 1), and estimates between the dashed lines are not assigned to either behavioural mode (the behavioural mode for these time steps could not be estimated with reasonable certainty, ie. $1.25 < b_t < 1.75$). These uncertain estimates of b_t correspond with the black circles in Fig. 1.

Figure 3. Stacked barplots of the proportion of observations within each depth, temperature or time bin obtained while turtle B.1 was transitting (black) or foraging (grey). The proportion of observations associated with behavioural modes that could not be estimated with reasonable certainty (see Fig. 2 caption) are displayed in white. The width of each bin is proportional to the total number of observations (all behavioural modes) within that range. The labels indicate the mid-point of each bin. Empty bins indicate no dives were observed in that range for any behavioural state over the duration of the movement pathway. Proportion of observations in each bin while foraging can be read from the top down on the right vertical axis. Labels on the colour scale are mid-points of the bins.

Figure 4. Differences between transitting and foraging for the four diving statistics, time at depth, time at temperature, maximum depth, and dive duration. Mean differences (and 95 % confidence intervals) are displayed for each of the 9 turtle tracks. Meta-analytic summaries (random effects mean with 95 % confidence interval) of the 9 individual estimates are displayed as solid diamonds on the bottom of each panel. Confidence intervals for the individual estimate were adjusted for temporal autocorrelation (see Methods for details). The trailing numerals in the turtle designations indicate separate annual migrations into northern waters for the same individual (see Methods for assumptions regarding independence).

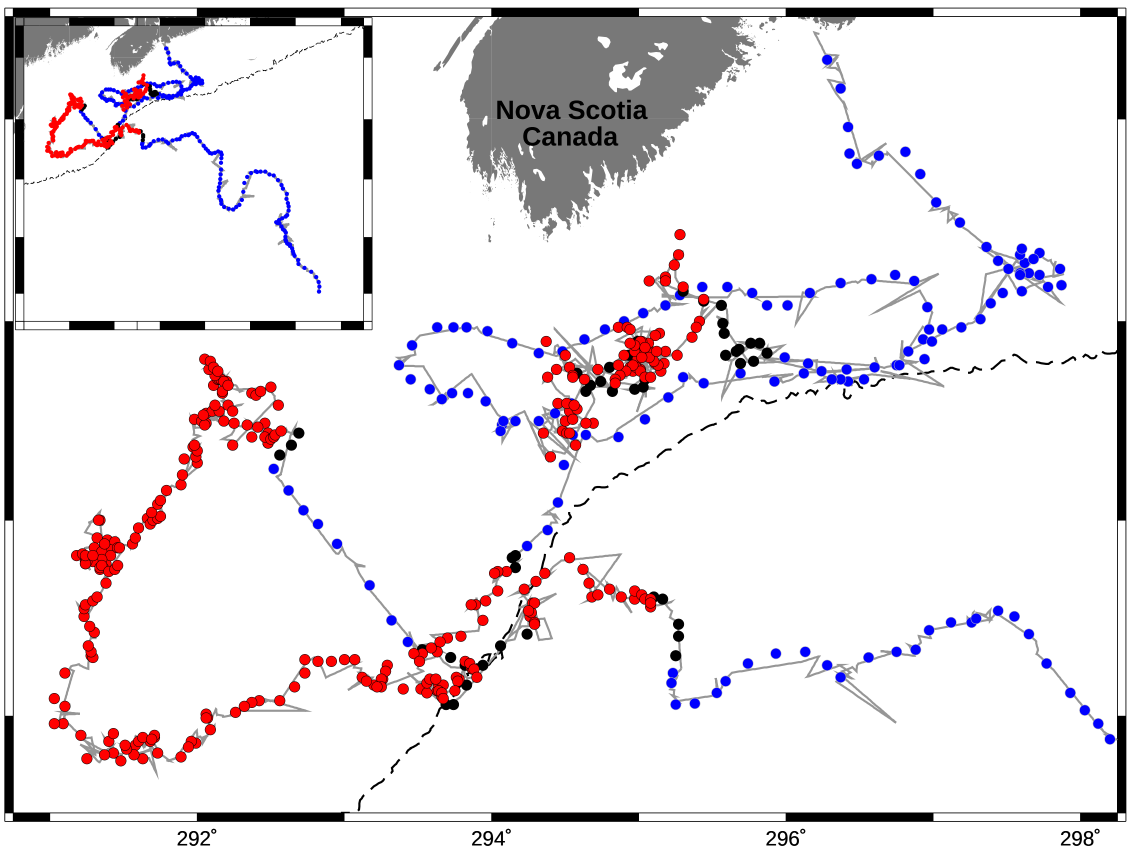


Figure 1:

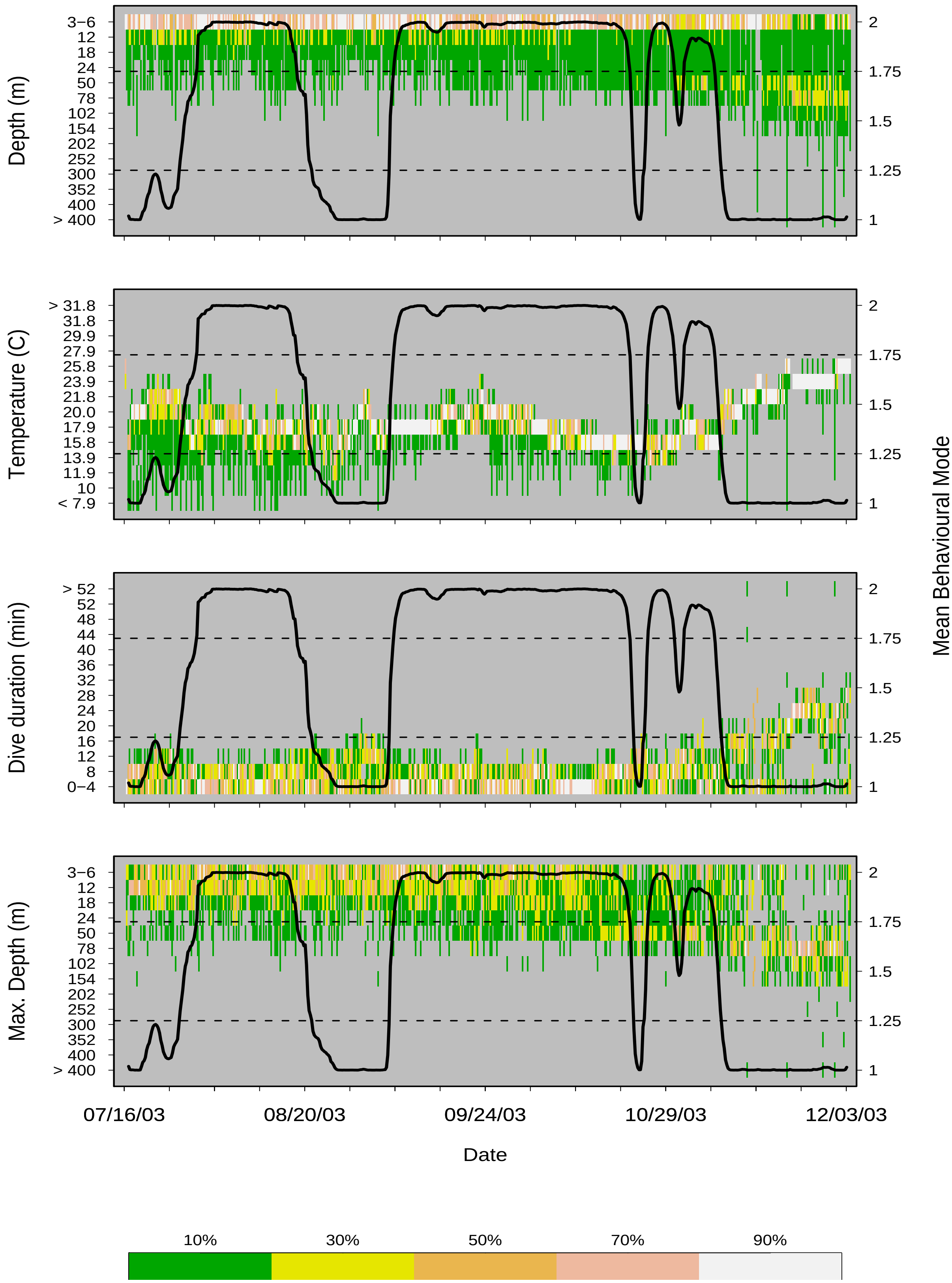
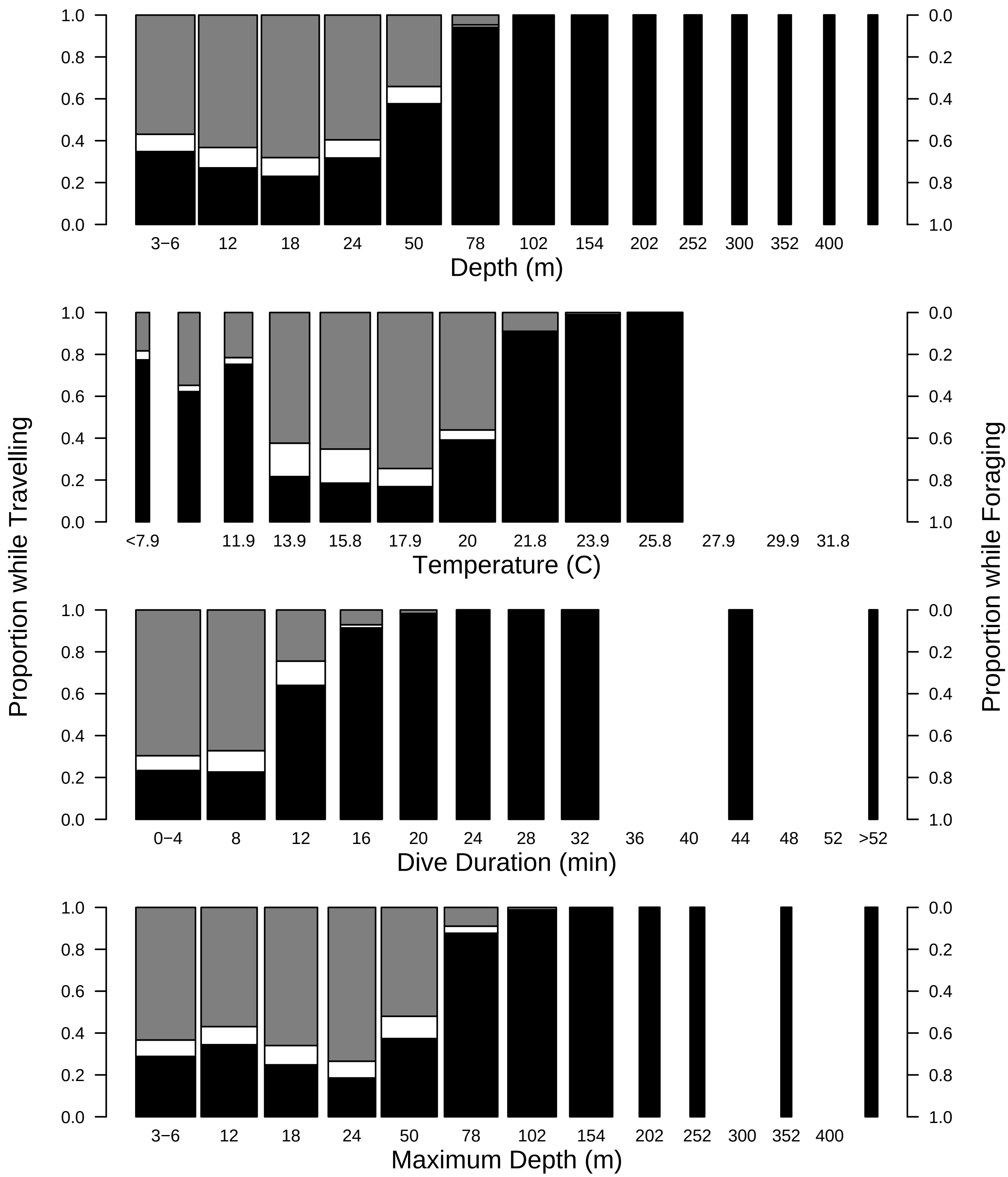

Depth (m)
Temperature (C)
Dive duration (min)
Max. Depth (m)
Mean Behavioural Mode
Date
07/16/03
08/20/03
09/24/03
10/29/03
12/03/03
10%
30%
50%
70%
90%

Figure 2:



Proportion while Travelling
Proportion while Foraging
1.0
0.8
0.6
0.4
0.2
0.0
3−6 12 18 24 50 78 102 154 202 252 300 352 400
Depth (m)
<7.9 11.9 13.9 15.8 17.9 20 21.8 23.9 25.8 27.9 29.9 31.8
Temperature (C)
0−4 8 12 16 20 24 28 32 36 40 44 48 52 >52
Dive Duration (min)
3−6 12 18 24 50 78 102 154 202 252 300 352 400
Maximum Depth (m)

Figure 3:

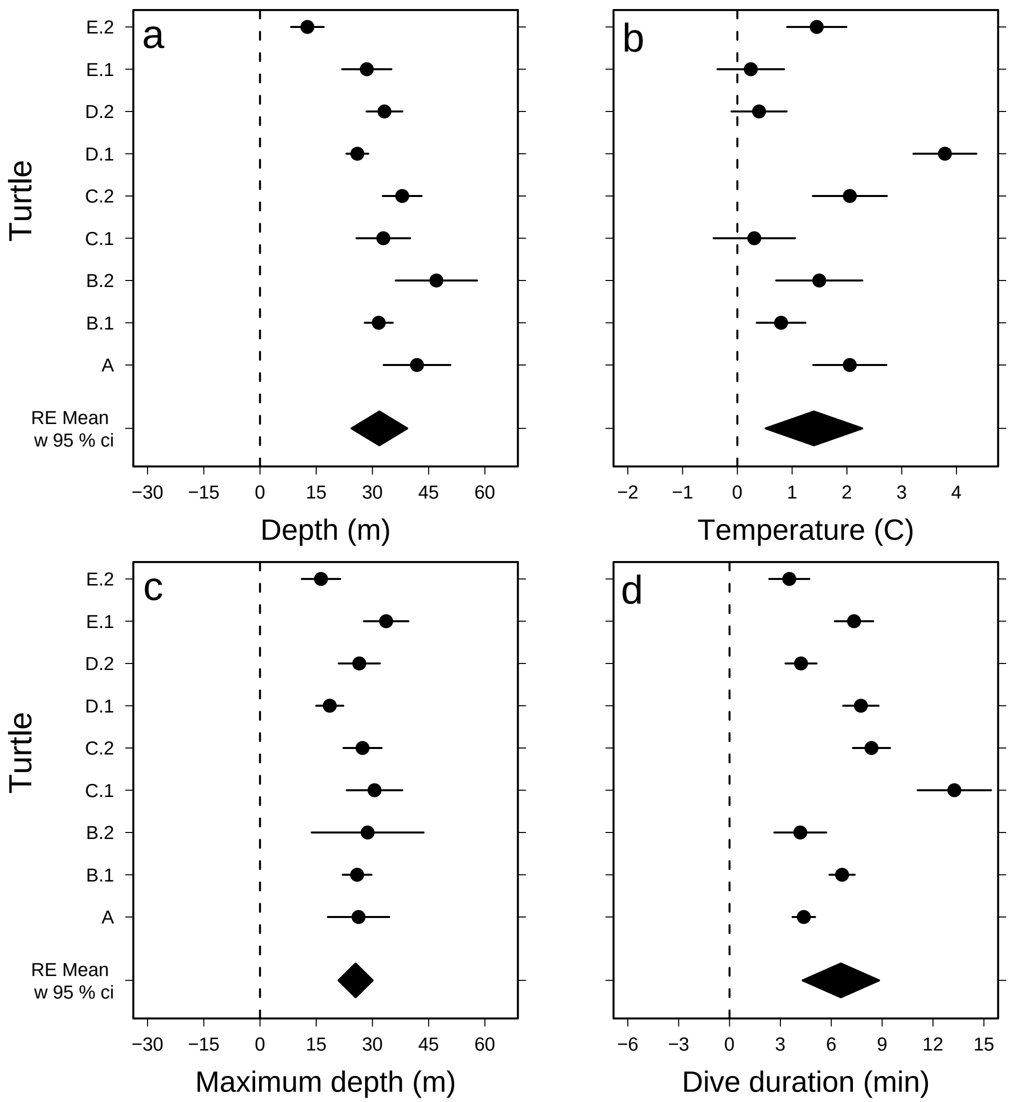

a
b
c
d
Turtle
E.2
E.1
D.2
D.1
C.2
C.1
B.2
B.1
A
RE Mean
w 95 % ci
−30 −15 0 15 30 45 60
Depth (m)
−2 −1 0 1 2 3 4
Temperature (C)
Maximum depth (m)
−6 −3 0 3 6 9 12 15
Dive duration (min)

Figure 4: