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Identifying and comparing phases of movement by leatherback turtles using state-space models

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Abstract

Leatherback turtles (*Dermochelys coriacea*) are currently critically endangered and could be on the verge of extinction within the Pacific Ocean. In 2004–7, satellite transmitters were attached to 46 female turtles nesting at Playa Grande, Costa Rica, to further investigate their distribution and movements in the eastern Pacific to improve conservation measures. State-space models (SSM) provide a valuable tool for modelling movement data by simultaneously accounting for measurement error and variability in the movement dynamics. Track simulations and a measure of the uncertainty for each position estimate allowed model performance with large amounts of missing satellite data to be assessed, as this is common for marine animals. A switching SSM was applied to the tracks of the turtles, which also provided an estimate of the behavioural mode at each location. This enabled the internesting period to be objectively defined based on a shift between these two modes. This switch occurred later than the last observed nesting event, indicating turtles did not immediately move offshore and the length of time and area that turtles utilise during internesting could previously have been underestimated. The movement parameters, mean turning angle and autocorrelation in speed and direction, for each mode were similar to those in the Atlantic Ocean, but the foraging phase was more prolonged and widely dispersed suggesting that food patches are less predictable in the Pacific. This may explain the long period between nesting seasons.

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1. Introduction

Over the last decade, developments in satellite telemetry have revolutionized our understanding of the distribution and movements of marine species (Gillespie 2001). However, positions are recorded sporadically and have associated errors (Vincent et al., 2002). A process of filtering (e.g. McConnell et al., 1992, Austin et al., 2003), to remove spurious locations, and interpolation (Tremblay et al., 2006), to obtain positions at regular intervals, therefore occurs prior to analysis. State-space modelling provides a valuable alternative by allowing the simultaneous incorporation of information on non-Gaussian position errors and the underlying behavioural processes to

obtain location estimates without discarding potentially valuable data points (Anderson-Sprecher and Ledolter 1991, Brillinger 1998, Jonsen et al., 2003).

There are at least three different approaches to getting improved information about the movements and behaviour of marine animals. The first is to use systems with higher accuracy, for example with GPS quality locations rather than the relatively poor accuracies provided by Argos. GPS data-loggers have already been successfully deployed onto turtles (Schofield et al., 2007) and studies with GPS tags that remotely relay locations via satellite are now underway (Lohmann et al., 2008-this issue). The second approach is to combine Argos quality location data with information on diving patterns to glean more about an animal's behaviour (e.g. Hochscheid et al., 2005). The third approach is to use improved data-analysis procedures with Argos data. This paper concerns this third approach.

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The application of switching state-space models (SSSM) enables movement parameters and behavioural modes to be estimated (Jonsen et al., 2005). These behaviours are classified using a first-difference correlated random walk. They have been defined as transiting and foraging, and the validity of this has been assessed with diving data from Atlantic leatherback turtles (*Dermochelys coriacea*) as direct behavioural observations were not available (Jonsen et al., 2007). However, changes in behaviour also occur between interesting and the postnesting migration in turtles (Hays et al., 1999). The end of interesting has previously been defined using the final nesting event (Troëng et al., 2005), but observational data may be incomplete or unavailable. A switch in the behavioural mode from the SSSM could therefore potentially be used to identify the cut-off between these two periods. This has not been investigated before as the SSSM has been applied to animals tagged during their foraging phase, which did not include the interesting period (Jonsen et al., 2007).

It has been hypothesized that the longer interval between nesting years for Pacific than Atlantic leatherback turtles might be caused by resource limitation (Wallace et al., 2006a) and that foraging strategies may differ between the two ocean basins (Wallace et al., 2006b). The movements of eastern Pacific leatherback turtles are also more restricted as they follow a narrow migration corridor after nesting (Morreale et al., 1996), whereas those in the Atlantic actively disperse (Ferraroli et al., 2004). The use of state-space models may help to identify the phases of movement by Pacific leatherbacks and determine how their behaviour and foraging strategy differs to those in the Atlantic.

This study applied a SSSM (Jonsen et al., 2007) to the satellite tracks of female eastern Pacific leatherback turtles to obtain improved position estimates and assess its use in defining the interesting period. The location of a subsequent behavioural switch was used to identify the boundary between the postnesting migration and foraging grounds. Parameter values defining the two behaviours were determined and also compared with those from an Atlantic population (Jonsen et al., 2007) to further understand behavioural differences between these populations.

2. Methods

2.1. Data

The data consist of ARGOS-derived surface locations from 46 female leatherback turtles tagged in January–February of 2004 ($n=27$), 2005 ($n=8$), and 2007 ($n=11$) with Sea Mammal Research Unit (SMRU) Satellite Relay Data Logger (SRDL) and Wildlife Computer (WC) Smart Position Only (SPOT) tags. The transmitters were attached using a harness during nesting at Playa Grande, Costa Rica (Eckert 2002). Animals were tracked for a mean of 263 days (range=55–562 days) and a mean distance of 8070 km (range=2161–17,133 km).

2.2. Switching state-space model (SSSM)

The SSSM developed by Jonsen et al. (2007) was applied to each of the individual turtle tracks, providing a position estimate

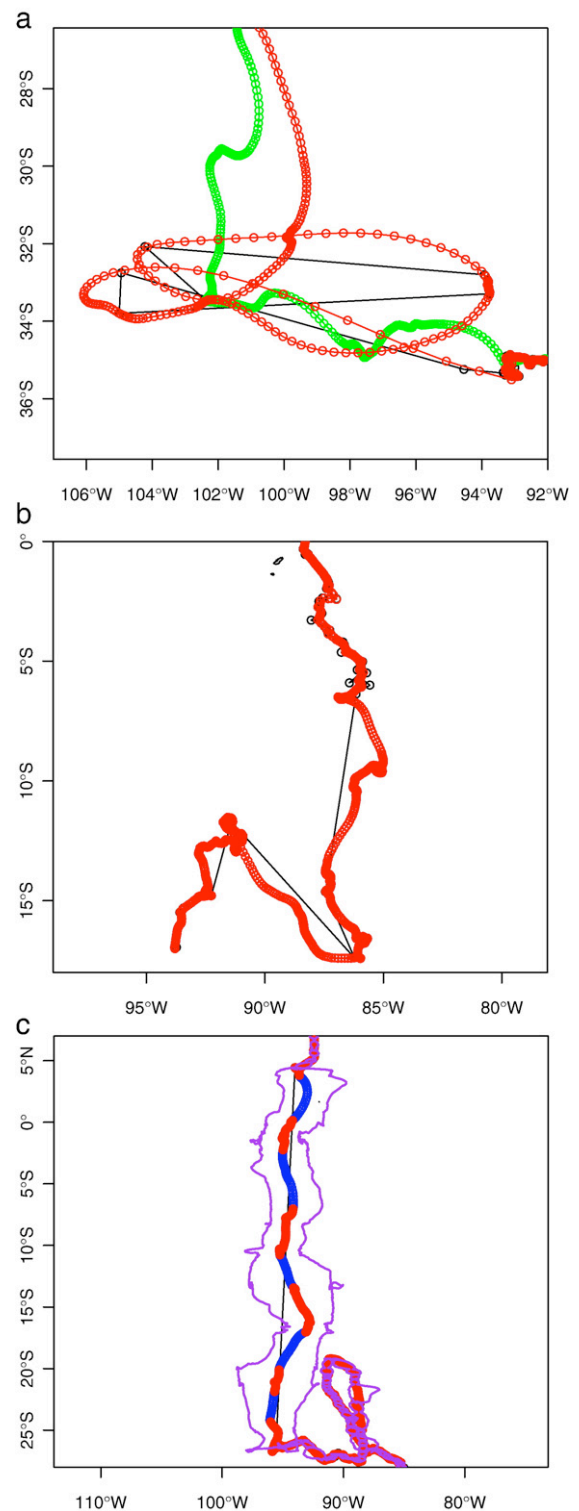


Fig. 1. Examples of the effects of missing satellite positions (black) on the SSSM estimates (red) when a) there are spurious satellite positions surrounded by missing data giving them greater weight on the SSSM estimates (the SSSM estimates when these positions are removed are shown in green), b) SSSM estimates begin to resemble earlier movements, such as curve patterns, as a result of prolonged periods with missing data and in c) alternation of the behavioural mode may also occur in such periods (the longitudinal 95% credible limits for the SSSM estimates, highlighting the wider limits when data is missing, are shown in purple).

at 6 hour intervals. This model allows position estimates to be inferred from observed data (satellite positions) by accounting for errors (measurement equation) and from dynamics of the movement process (transition equation). As in Jonsen et al. (2007), the measurement equation estimation errors for each location class were based on published data from tags on captive grey seals (Vincent et al., 2002). Similar priors were also placed on the model parameters. When satellite positions were missing, linearly interpolated positions were used as the initial values. The model was fit to each individual track with two chains running in parallel a total of 20,000 Markov Chain Monte Carlo (MCMC) samples, the first 15,000 were discarded as a burn-in and the remaining samples were thinned, retaining every 10th sample to reduce autocorrelation.

Since all of the tracks had periods with fewer raw satellite positions than the 6-hourly interval at which the SSSM positions were being estimated, the impact of missing data on the accuracy of the SSSM estimates was assessed. Two tracks, each with 100 position points, were generated with a starting location of 10°N, 90°W. Sequential positions were assigned by randomly selecting a distance and heading from the distributions produced by the real 6 hourly SSSM turtle estimates and then using the next 98 values so that a similar autocorrelation structure was retained. The headings were selected from positions that had behavioural mode 1 to represent relatively straight movement and behavioural mode 2 for curved movement. These were defined as the true tracks and noise was then added to simulate that of ARGOS-derived locations. More than half of the turtle positions had location quality class B and these errors were therefore applied to all positions by randomly selecting from two normal distributions (mean accuracy = 7.00 km, $SD_{\text{latitude}} = 5.23$ km, $SD_{\text{longitude}} = 7.79$ km (Hays et al., 2001)). This resulted in tracks with a linearity index (straight line distance from first to last position divided by the total distance travelled) of 0.7 for the straight track and 0.3 for the curved track. The SSSM was applied and then positions were sequentially removed from the centre of the tracks and the model run again on each of these incomplete datasets. The difference in the mean SSSM estimate

and the true location for each point was calculated to determine the mean absolute error.

Although a high number of MCMC samples were used as a burn-in to ensure convergence, the number of samples on which the final inferences were based was smaller ($n=500$) than that generated by Jonsen et al. (2007) who used 30,000 iterations, 10,000 sample burn-in and retained every 5th sample ($n=4000$). This was done to reduce the amount of computing time and memory required as there were many long tracks in the dataset. However, to ensure that this did not reduce the accuracy of the estimates, the SSSM was also run with the higher number of samples on the two complete simulated tracks described above. The difference in the mean absolute error and width of the 95% credible limits was compared for the two different numbers of samples.

2.3. Analyses

Posterior distributions for the movement parameters θ , mean turning angle, and γ , autocorrelation in speed and direction, indexed by the behavioural mode were output from the model. The model included two behavioural modes based on a switching correlated random walk (Jonsen et al., 2005). If there was no overlap in the values of θ and γ for the two modes, this indicated that use of the switching model had been appropriate. A histogram of mean behavioural mode for all of the tracks combined confirmed an appropriate cut-off value for the two behavioural modes. The number of tracks that had a clear behavioural switch between internesting and the postnesting migration was determined and the timing of this switch was compared to the last nesting event recorded by visual observation at the beach. The number and location of behavioural switches was compared between individuals and used to assess whether there were specific phases in their movement. The parameters θ and γ were compared between individual tracks that exhibited different movement patterns and with the results from a SSSM performed on five leatherback turtles from the Atlantic (total of nine track segments) (Jonsen et al., 2007) to see if there was any indication of differences in foraging strategies.

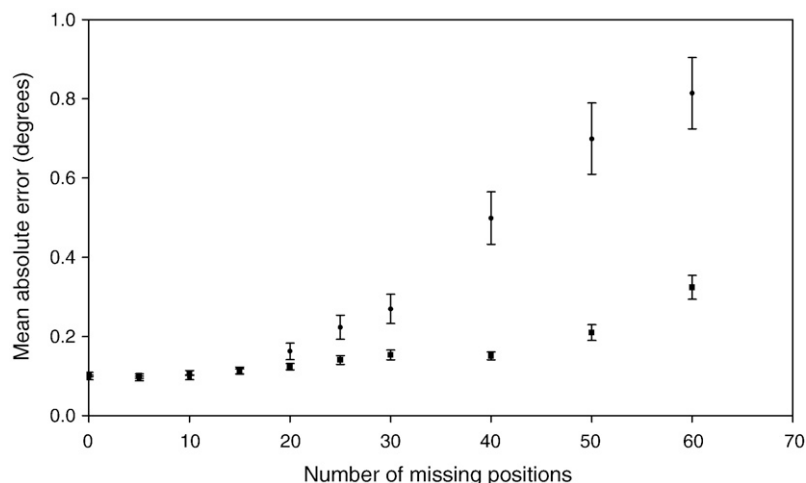


Fig. 2. Mean absolute error (and SE) of SSSM mean position estimates in relation to the number of raw locations missing for a relatively straight (linearity index = 0.7) and curved (linearity index = 0.3) track shown as squares and circles respectively.

3. Results

The highest number of raw satellite positions per day occurred during the first two months after deployment (mean=6.3 positions per day). Following this period, the number of positions significantly declined with time to a monthly average of 0.8 positions per day ($F=5.789$, $df=1,9$, $P<0.05$). However, several tracks had prolonged periods with no recorded satellite positions. The maximum number of consecutively missing days varied from 1 to 241 (median=18 days) per individual track. Some effects on the SSSM estimates that were noted were:

1. Raw satellite positions have more weight on SSSM estimates when they are surrounded by missing data (Fig. 1a). This can lead to less accurate estimates and in extreme cases it may be worth removing these spurious satellite positions before applying the model. Sensitivity of the model to the position initial values meant that using a linearly interpolated position where raw data were missing helped to ensure convergence of the model and reduce the 95% credible limits.
2. SSSM estimates begin to resemble patterns of earlier movement if there is a long period of missing data (Fig. 1b). The model uses information prior to the missing location in determining the next position estimate. When the period of missing data is prolonged this can lead to earlier curves being repeated.
3. Behavioural mode estimates become unreliable if there are long periods of missing data and the mean behavioural mode approaches 0.5 resulting in alternations between the two modes (Fig. 1c).

The track simulations showed that the accuracy of the SSSM estimates declined as the number of raw positions missing increased (Fig. 2). The errors were greater for the more curved track and rose steeply when more than 30 consecutive positions were missing. The error remained less than 0.2° with up to 40 positions missing for the relatively straight track. The position of missing data within the track and the total length of the track, which influences the amount of information available to the model, will also have an impact on the accuracy of the estimates. It is therefore important that the SSSM results are carefully checked against the raw data to make sure there are no obvious anomalies.

In a comparison of the different number of samples, the mean absolute location error for the SSSM applied to the two complete simulated tracks was 0.103° and 0.097° for the straight and curved tracks respectively for both 500 and 4000 samples ($SD=0.006^\circ$ in all cases). This indicated that only using 500 samples had not reduced the accuracy of the mean position estimates as there had been sufficient convergence of the model with 15,000 samples as a burn-in. There was only a slight increase in the mean width of the 95% credible limits (0.004° for the straight track and 0.011° for the curved track) using the smaller number of samples.

The use of the SSSM was appropriate for all of the tracks as there was no overlap in the 95% credible limits (CL) for θ in the two behavioural modes and there was only marginal overlap

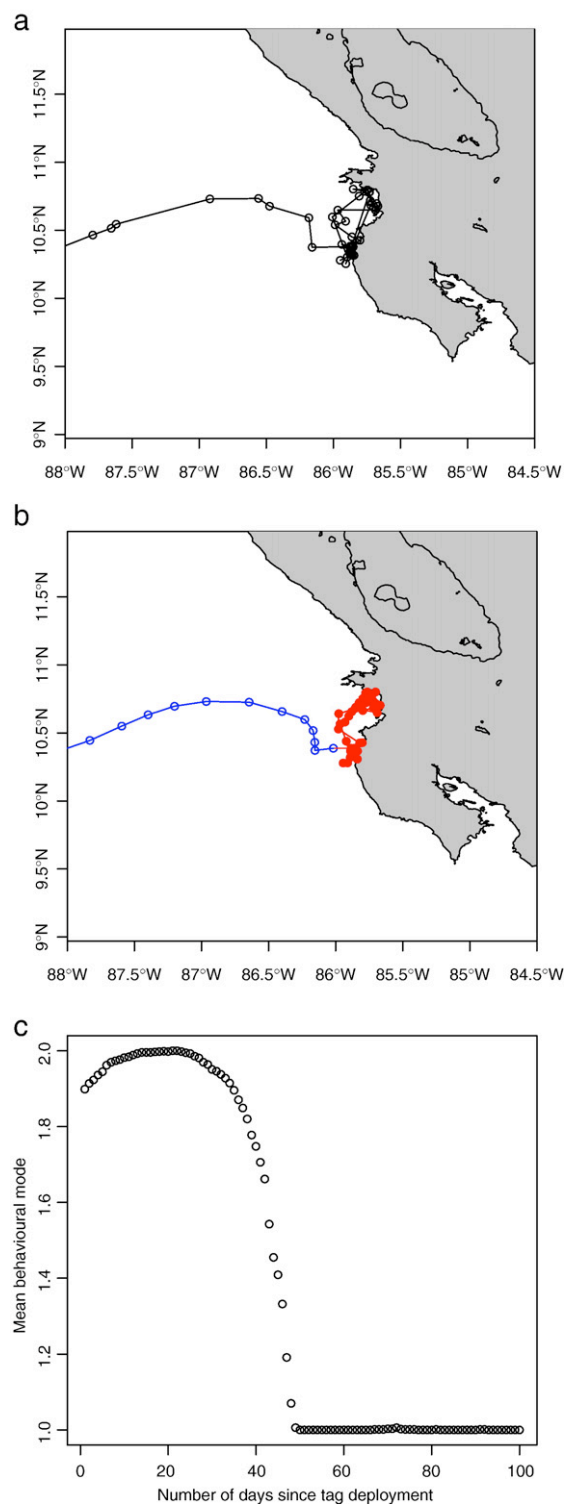


Fig. 3. a) The early part of a raw satellite track (black), b) behavioural mode 1 (blue) and 2 (red) for the SSSM position estimates and c) change in mean behavioural mode with time showing the behavioural change between interesting (mean > 1.5) and migration (mean < 1.5).

(mean=9%) for γ in 18 tracks. The distribution of the mean behavioural mode for all of the tracks combined was strongly bimodal. Based on this, values less than 1.5 were assigned mode

1 and greater than 1.5 as mode 2. In 32 of the tracks (70%), there was a switch (defined as 3 or more consecutive positions in the new mode) between these two behavioural modes as the turtles moved offshore following nesting (Fig. 3). This switch occurred later than the last observed nesting event (mean = 18 days, 95% CI = 6 days), which on average was observed on 10 February, whereas the mean date for the SSSM behavioural switch was 28 February. A time lag therefore seemed to occur between the behaviour switch from interesting to migration, and the last nesting event. However, final nesting could also have occurred after the end of the observation period (March).

There were differences in the number of behavioural switches that occurred between tracks, but two main patterns emerged (Fig. 4). Nearly a quarter of the tracks had predominantly one behavioural mode (>95% of locations) and 46% of the tracks had two main switches in behavioural

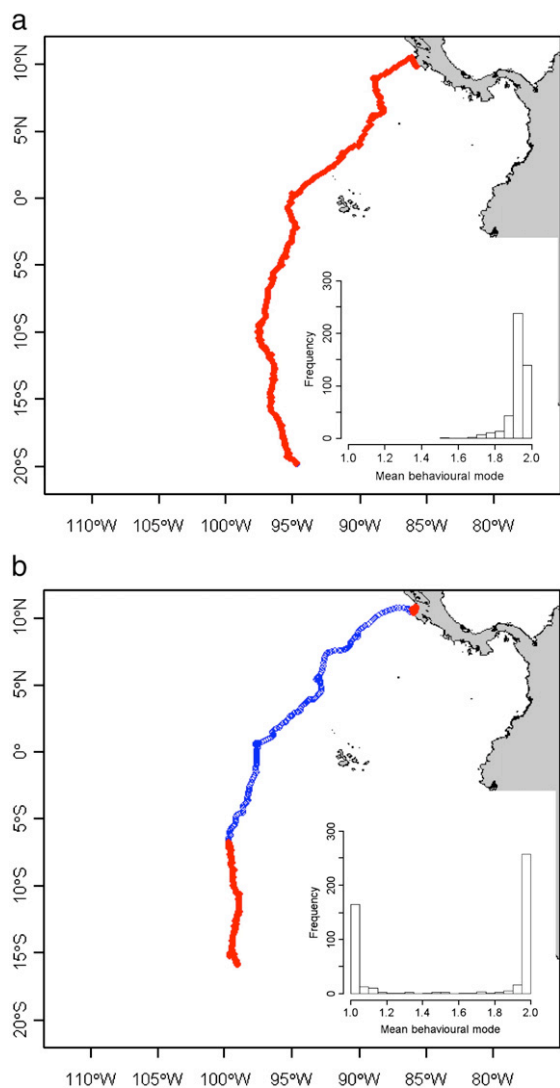


Fig. 4. Map of SSSM position estimates and histogram of mean behavioural mode showing examples of the two major movement patterns a) predominantly one behavioural mode and b) two main behavioural switches. Behavioural mode 1 (postnesting migration) is shown in blue and mode 2 (interesting and foraging) in red.

Table 1

Mean (and SE) quantiles of the marginal posterior distributions for the movement parameters θ_k (mean turning angle in radians) and γ_k (autocorrelation of direction and speed) for tracks from the Pacific with one behavioural mode ($n=11$) and those with three behaviours (mainly two behavioural switches) ($n=21$)

Parameter	Posterior quantiles	Pacific		Atlantic
		1 behaviour	3 behaviours	
θ_1	0.025	-0.74 (0.08)	-0.40 (0.11)	-0.19 (0.02)
	0.5	0.02 (0.03)	-0.02 (0.03)	-0.02 (0.01)
	0.975	0.78 (0.07)	0.29 (0.03)	0.15 (0.03)
θ_2	0.025	2.66 (0.06)	2.64 (0.08)	2.53 (0.18)
	0.5	3.27 (0.05)	3.25 (0.11)	3.53 (0.17)
	0.975	3.94 (0.10)	3.79 (0.13)	4.41 (0.19)
γ_1	0.025	0.63 (0.01)	0.56 (0.01)	0.61 (0.02)
	0.5	0.74 (0.00)	0.66 (0.01)	0.70 (0.02)
	0.975	0.84 (0.00)	0.76 (0.01)	0.79 (0.02)
γ_2	0.025	0.27 (0.03)	0.29 (0.02)	0.18 (0.01)
	0.5	0.42 (0.03)	0.42 (0.03)	0.31 (0.02)
	0.975	0.57 (0.03)	0.55 (0.02)	0.46 (0.03)

These are compared with values for the Atlantic ($n=9$). The subscript refers to the behavioural modes 1 and 2.

mode. The remaining tracks had long sections with missing data, which made the behavioural estimates unreliable for these periods, or the two behavioural modes were highly interspersed along the track.

The pattern with the two behavioural switches indicated three phases of movement: interesting, postnesting migration and foraging. Interesting and foraging were indicated by behavioural mode 2 and the postnesting migration by mode 1 (Fig. 4b). The mean positions of these distinct behavioural switches occurred at 10.34°N, 86.21°W (near the coast) and 8.27°S, 103.30°W (southwest of the Galapagos Islands) respectively. Animals generally began foraging in late March to the end of April after nesting. There was much greater consistency in the latitude ($SD=4.11^\circ$) at which this began than in longitude ($SD=10.56^\circ$). The location of the foraging positions extended as far south as 37.69°S and between 82.58 and 125.57°W. There was no overlap in the movement parameters θ and γ for behavioural modes 1 and 2, even when only one behavioural phase predominantly occurred within a track (Table 1). Mode 1, occurring during the postnesting migration, had a turning angle centred close to zero and high autocorrelation in speed and direction, whereas in mode 2, during interesting and foraging, the turning angle was nearly 180° indicating an almost complete reversal in direction. The values of θ and γ for the Pacific and Atlantic leatherback turtles were very similar with a high level of overlap in the 95% credible limits for each of the behavioural modes (Table 1).

4. Discussion

Although leatherback turtles could be on the verge of extinction within the Pacific (Spotila et al., 2000), the majority of satellite tracking research has previously focused on Atlantic populations (Luschi et al., 2003, James et al., 2005b, Hays et al., 2006). Turtles may undergo long pan-oceanic migrations between their nesting and foraging grounds (Nichols et al.,

2000, Hays et al., 2004b), but our knowledge of the movements of these animals in the Pacific Ocean is relatively poor. The application of the state-space approach has provided a valuable tool for elucidating the movements of these animals, objectively defining their phases of movement and comparing these behaviours between two populations.

Much of our information on the biology of turtles has so far been achieved through studies on nesting female turtles (Reina et al., 2002). During this reproductive season the animals use a restricted area in the vicinity of the nesting beach, which is likely to be an energy minimising mechanism (Hays et al., 1999). Turtles are particularly vulnerable to disturbance and injury during this period and protecting these areas should be a conservation priority (Zbinden et al., 2007). However, the low spatial and temporal resolution of satellite data may make it difficult to determine their exact movements and this was greatly improved by using the SSSM position estimates. The boundary between this phase and the postnesting migration may also be unclear from the raw satellite data. Making visual observations of nesting events is labour intensive and often restricted to the peak of the nesting season. It is also of most relevance to coastal conservation management when the period of restricted movement ends and animals migrate offshore. One method to circumvent poor location accuracy from Argos tags is to supplement analysis of Argos data with examination of haul-out data relayed from the tags to indicate turtles have come ashore to nest (Georges et al., 2007). Similarly, the SSSM approach allows improved estimation of the internesting behavioural phase. The SSSM behavioural switch indicated that this did not begin immediately after the final nesting event and using this information only could underestimate the length of time and area that the turtles utilise during internesting. The tracks in which no clear switch occurred tended to be those tagged late in their nesting season or that were only tracked for a short period. The amount of data may therefore have been insufficient for the model to discern between the different phases. These tracks were predominantly in the foraging mode and could also indicate that animals were searching for food as they travelled, which has previously been suggested based on dive patterns (Hays et al., 2006).

As the animals moved offshore, a distinct change in behavioural mode was detected that was characterized by relatively straight movement and high autocorrelation in travel speed and direction. Using state-space models, Jonsen et al. (2006) identified there was also a change in the diel pattern of travel rates between foraging and migrating in the Atlantic. The movement parameters for the two behavioural modes (Table 1) were very similar to those of Atlantic animals (Jonsen et al., 2007) indicating similar responses to efficiently migrate and forage. However, there seemed to be two key differences in their strategies. Firstly, all of the turtles in this study migrated towards the eastern South Pacific whereas turtles nesting in French Guiana and Suriname dispersed throughout the North Atlantic (Ferraroli et al., 2004). This is also in contrast to the migration of leatherback turtles nesting in Indonesia, which may travel across the entire North Pacific to reach their foraging areas off North America (Benson et al., 2007). Secondly, there

are specific foraging areas off western Africa, Canada and northeastern USA, and in the northeastern Atlantic and individuals appear to maintain some regional fidelity (James et al., 2005a, Hays et al., 2006). The foraging phase for the eastern Pacific turtles was relatively prolonged (beginning only a couple of months after nesting and up to the end of the tag transmissions) and widely dispersed, suggesting food was less predictable and searching was required over larger areas. The area south of 8°S, the South Pacific Gyre, is known to be highly oligotrophic and strongly governed by the El Niño Southern Oscillation (McClain et al., 2004). This interannual variability and consequent impact on food resources may mean that leatherback turtles in this region take longer to build up the energy reserves required for egg production and could consequently explain the long period of time (mean=3.7 years, range=2–7 years) between nesting seasons for individual turtles (Reina et al., 2002, Saba et al., 2007).

During their migration in the eastern Pacific, the leatherback turtles moved through a complex system of strong equatorial currents (Kessler 2006). It is therefore possible that the apparent change in behavioural mode was largely an effect of the currents on the turtles' movement. Further investigation of this could be conducted by analyzing tracks corrected for ocean currents (Gaspar et al., 2006) or including covariates within the state-space model. However, the two tracks in Fig. 4 are from the same year and thus would have been similarly affected by the currents, but different behavioural mode patterns occurred. This suggests that there was an actual change in behaviour, but there was variability between individuals. Confirmation of this could be provided by analysing the diving data from the tags (Hays et al., 2004a). The identification of three behavioural phases suggests that improvements could be made by applying a 3-state switching state-space model. Although the foraging paths of many turtles were not as linear as that in Fig. 4b, the mean turning angle did seem to be less than that during internesting and may be better described by a third behavioural mode.

Reduction in accuracy of the SSSM estimates occurred when there were prolonged periods of missing satellite data. Surfacing behaviour, biofouling or tag defects can result in periods of weeks or even months with missing or sporadic locations (Hays et al., 2007). The severity of these problems will vary with the species and location and it is essential to investigate the regularity with which positions have been recorded before any further analysis is conducted. Using a linearly interpolated position as an initial value proved the best method of obtaining reasonable SSSM estimates in these situations. Examining the 95% credible limits for the position estimates also allowed the uncertainty surrounding each position to be determined. Whether this is acceptable for the study or the data should instead be divided into track sections can then be decided. This uncertainty information can also be incorporated into subsequent habitat analysis.

In essence the SSSM allows an objective definition of the different behavioral phases such as migration versus foraging which have previously been inferred subjectively for leatherbacks based on changes in speed of travel and diving behaviour (Hays et al., 2006). Thus, using SSSM is a valuable approach to

analyzing telemetry data. The resulting tracks are more accurate and reveal changes in behaviour of the turtles. When this approach is combined with a careful examination of the corresponding oceanographic conditions we will be able to obtain a clearer picture of the mechanisms that are responsible for the movements of leatherbacks and closer to predicting the behaviour of these animals in their natural habitat.

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