

## MODELING LOGGERHEAD TURTLE MOVEMENT IN THE MEDITERRANEAN: IMPORTANCE OF BODY SIZE AND OCEANOGRAPHY

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**Abstract.** Adapting state–space models (SSMs) to telemetry data has been helpful for dealing with location error and for modeling animal movements. We used a combination of two hierarchical Bayesian SSMs to estimate movement pathways from Argos satellite-tag data for 15 juvenile loggerhead turtles (*Caretta caretta*) in the western Mediterranean Sea, and to probabilistically assign locations to one of two behavioral movement types and relate those behaviors to environmental features. A Monte Carlo procedure helped propagate location uncertainty from the first SSM into the estimation of behavioral states and environment–behavior relationships in the second SSM. Turtles using oceanic habitats of the Balearic Sea ( $n = 9$  turtles) within the western Mediterranean were more likely to exhibit “intensive search” behavior as might occur during foraging, but only larger turtles responded to variations in sea-surface height. This suggests that they were better able than smaller turtles to cue on environmental features that concentrate prey resources or were more dependent on high-quality feeding areas. These findings stress the importance of individual heterogeneity in the analysis of movement behavior and, taken in concert with descriptive studies of Pacific loggerheads, suggest that directed movements toward patchy ephemeral resources may be a general property of larger juvenile loggerheads in different populations. We discovered size-based variation in loggerhead distribution and documented use of the western Mediterranean Sea by turtles larger than previously thought to occur there. With one exception, only individuals  $>57$  cm curved carapace length used the most westerly basin in the Mediterranean (western Alborán Sea). These observations shed new light on loggerhead migration phenology.

**Key words:** Alborán Sea; animal movement; *Caretta caretta*; endangered species; environment–behavior relationships; hierarchical Bayes; juvenile loggerhead behavior; loggerhead sea turtle; Mediterranean Sea; oceanography; satellite telemetry; state–space model.

### INTRODUCTION

Spatially explicit animal-movement models are increasingly used to understand habitat selection (e.g., Arthur et al. 1996, Hjermann 2000, Fauchald and Tveraa 2003, 2006, Morales et al. 2004, Preisler et al. 2004, Pinaud and Weimerskirch 2005, Breed et al. 2006, Suryan et al. 2006). This is partly due to the difficulty in meeting model assumptions of conventional selection analyses that rely on a spatially implicit framework to assess whether habitat use is nonrandom with respect to the available habitat (Manly et al. 2002, Alldredge and Griswold 2006). For example, many conventional analyses require well-defined habitat categories within well-defined use areas at individual or population levels.

However, both habitats and animal use areas are difficult to define in many systems. In marine pelagic systems, resource distributions are spatially and temporally dynamic or hierarchically structured (Valiela 1995, Fauchald and Tveraa 2003, 2006, Pinaud and Weimerskirch 2005), and far-ranging migratory animals—such as sea turtles—are not tied to central use areas for most of the year (e.g., James et al. 2005, Eckert 2006, Polovina et al. 2006). Conventional analyses also assume constant habitat availability and independence of observed animal locations. However, availability of habitat for an individual may vary as a function of its current location within large or undefined use-areas (Arthur et al. 1996, Hjermann 2000, Rhodes et al. 2005), or because the environment itself changes. Moreover, animal locations from the same individual are rarely independent, but rather, produce a complex, autocorrelated time-series that may comprise multiple types of movement behavior (Fauchald and Tveraa 2003, 2006,

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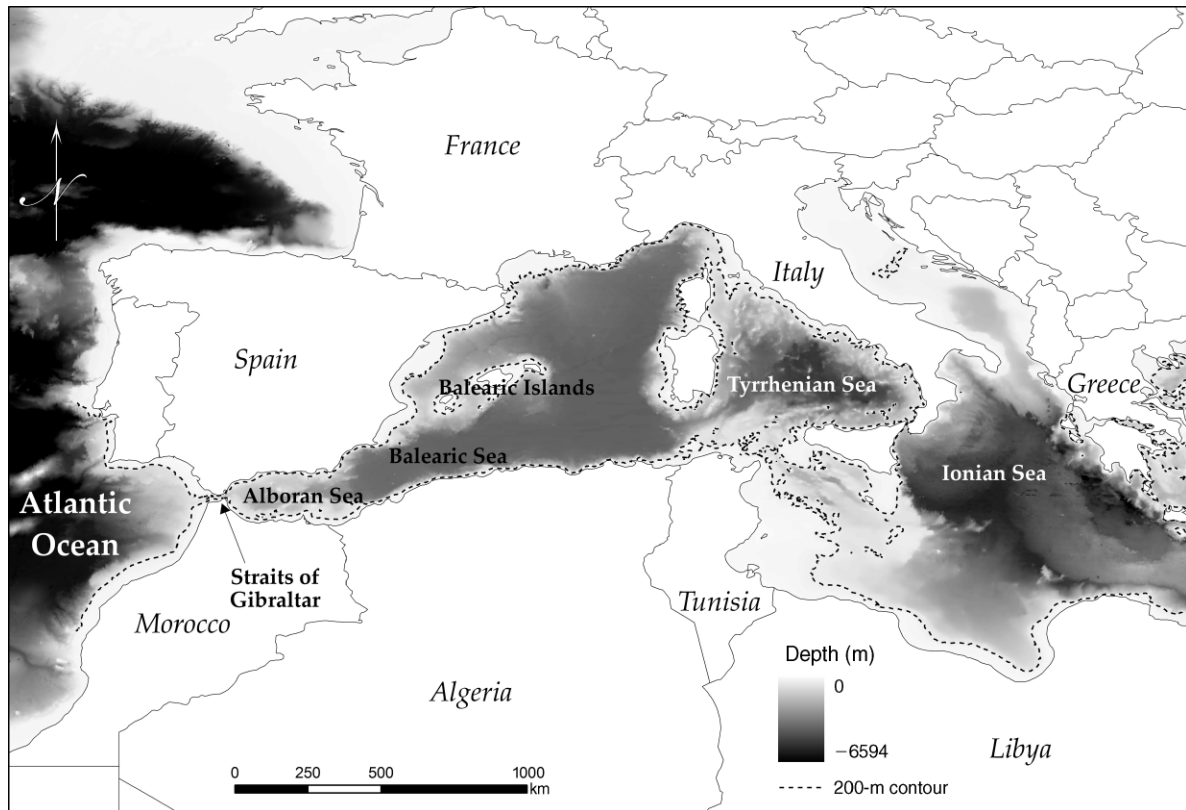


FIG. 1. Map of the western Mediterranean Sea, including regional sea names and bathymetry.

Morales et al. 2004, Frair et al. 2005, Jonsen et al. 2005, Sibert et al. 2006).

Spatial location error inherent to telemetry data poses additional challenges for studying habitat selection. For example, Argos satellite-telemetry data capture detailed movement patterns of individuals over potentially long time scales and large spatial regimes (Argos 2000), but these data are recorded irregularly in time with varying and sometimes large degrees of spatial error (Hays et al. 2001, Vincent et al. 2002, White and Sjöberg 2002). Traditionally, locations known to contain extreme error have been filtered using a priori criteria (Argos 2000, Austin et al. 2003, Douglas 2006), and then analyses or movement descriptions have been based on remaining points. However, such filters may lead to information loss, and at the same time ignore location error for points that are not removed by the filter (Jonsen et al. 2005).

Adapting state-space models to location data has been particularly helpful for modeling animal movements while dealing with location error or temporal data gaps (Anderson-Sprecher 1994, Sibert et al. 2003, 2006, Morales et al. 2004, Jonsen et al. 2005, 2006, Royer et al. 2005, Nielsen et al. 2006). State-space models link two types of equations: a transition equation, in which an unobservable state variable (such as an animal's true location or behavioral state) changes through time

according to a Markov process, and an observation equation that relates the state variable to the observed data (e.g., locations recorded by telemetry methods, or metrics characterizing successive movements). The goal is to estimate the state variable. Applied to Argos (or other telemetry) data, state-space models may be used to estimate true animal locations at regular time intervals (Jonsen et al. 2005, 2006, 2007). These improve on a priori filters because no locations are discarded (information loss is minimized), nor is location error ignored for any point (Jonsen et al. 2005).

The Alborán Sea, extending from the Straits of Gibraltar in the west to the Balearic Sea (Fig. 1), has the highest biodiversity within the Mediterranean Sea due to a combination of deep water and oceanic mixing brought about by the flow of Atlantic Ocean waters through the Straits (Tintoré et al. 1988, Rodriguez et al. 1994, Send et al. 1999). The region is an important developmental area for thousands of juvenile and subadult loggerhead sea turtles (*Caretta caretta*) that originate from nesting areas in the western Atlantic and eastern Mediterranean (Laurent et al. 1998, Carreras et al. 2006) and congregate in pelagic habitats (Camiñas and de la Serna 1995, Camiñas 1996, de Segura et al. 2006). This region also supports large fishing operations that comprise a diverse array of gear types, including longlines, driftnets, trawlers, and trammel nets, in which

thousands of juvenile loggerheads are incidentally captured or killed annually (e.g., Aguilar et al. 1995, Silvani et al. 1999, Carreras et al. 2004, Tudela et al. 2005). Given the endangered status of the Atlantic loggerhead (IUCN 2006), reducing mortality of the species in the western Mediterranean is vital to this population's conservation (Margaritoulis et al. 2003, de Segura et al. 2006). While time–area fishing closures might reduce loggerhead fishery interactions, little is known about how juvenile loggerheads make use of their environment in the region. Foraging habitats have not been characterized, nor have movement patterns been adequately explained in an oceanographic context.

Several studies have used Argos telemetry to examine loggerhead movements in the Mediterranean, but these have been primarily descriptive and have focused on inter-nesting movements of adult females or migratory patterns, not on movements of resident juveniles (Camiñas 1997, Bentivenga 2002, Hays et al. 2002, Houghton et al. 2002, Godley et al. 2003). Cardona et al. (2005) and Revelles et al. (2007) did investigate habitat use and movements of juveniles in the western Mediterranean on a finer temporal scale, and they defined habitats on the basis of three bathymetric depth classes. However they used conventional selection analyses, which can be subject to the potential problems described above, and they conducted their analyses separately for individuals in their data set, which precluded the evaluation of population-level patterns. Bentivenga et al. (2007) investigated effects of currents on loggerhead movement, but inference was limited by small sample size and availability of data for currents. Such studies have advanced our understanding of loggerhead movements in the western Mediterranean, but there remains a serious lack of knowledge about the linkage between environmental features and the spatio-temporal distributions of turtles.

More studies are needed—in this system and others—that investigate habitat use in a spatially-explicit analytical framework and that account for issues of location error, and time-series data composed of multiple behaviors, and that also address individual variation in environment–behavior relationships (Thomas et al. 2006). Based on Argos satellite-tag data from 18 juvenile loggerheads captured in the western Mediterranean, we first qualitatively evaluated large-scale relationships between turtle size and space use. Turtle size corresponds to developmental stages characterized by distinctive feeding and habitat ecologies (Bolten 2003). Then, we used hierarchical Bayesian state–space models to fit Mediterranean loggerhead pathways to the satellite-tag data, and to probabilistically assign locations in the pathways, based on movement characteristics, to one of two behavioral movement types that were assumed to be dependent on environmental features and turtle size class. Our work builds upon previous marine state–space applications by modeling changes in animal movement behavior explicitly as a function of dynamic

oceanographic variables within a hierarchical framework and by addressing location uncertainty in evaluating environment–behavior relationships. We feel this is an important step toward understanding habitat utilization of juvenile loggerheads in the Mediterranean Sea, and is applicable to other marine animal populations that utilize highly dynamic and ephemerally distributed habitats. Our study yields novel and important insights into the complex migration phenology of an endangered species.

## METHODS

### *Capture and tagging of turtles*

Between 6 July 2004 and 9 August 2005 juvenile loggerhead turtles were captured along a 520-km-long section of the Spanish Mediterranean coast. Turtles observed at the surface were captured by hand by an observer leaping from an inflatable boat. Turtles were tagged in the second scale of each front flipper with an inconel model 681s flipper tag (National Band and Tag Company, Newport, Kentucky, USA), and a passive integrated transponder (PIT) tag (Avid Microchip ID Systems, Folsom, Louisiana, USA) was inserted into the triceps muscle. Turtles were measured (curved carapace length and width), weighed, and scanned for internal fishing hooks with a metal detector (Zircon MT6; Zircon, Campbell, California, USA). If a hook was detected, the turtle was released and was not involved in the study.

All turtles received a SDR-T16 or a SPOT4 platform transmitter terminal (PTT) (Wildlife Computers, Redmond, Washington, USA); these utilize the Argos satellite telemetry system (Argos 2000) for data relay and location determination. Transmitters were mounted to the highest part of the carapace, usually over the second vertebral (midline) scute (see Plate 1). The mount area was cleaned with an abrasive plastic pad and wiped with alcohol, and sanded lightly. The base of the PTT was coated with a 1-cm-thick mixture of 45 mL of A20/1000 high pressure borosilicate micro-balloons (3M Corporation, Saint Paul, Minnesota, USA) and 250 mL of West Systems number 105 epoxy combined with number 205 hardener (West Systems, Watsonville, California, USA). Use of the borosilicate micro-balloons thickened the resin and substantially reduced the temperature of curing, thereby preventing damage to the carapace and temperature-related discomfort to the animal. Once the PTT was in place, a mixture of West Systems number 105 epoxy and number 205 hardener was used to apply fiberglass cloth over the transmitter and mount area. When the resin cured, the transmitter and overlying resin were coated with dark blue antifouling paint (Interlux Micron 66; International Paint, Union, New Jersey, USA).

### *State–space models*

We used a combination of two state–space model frameworks. In the first stage of analysis, we used the

framework developed by Jonsen et al. (2005) to construct best-fit animal trajectories from Argos satellite data. The state variable was a two-dimensional vector,  $\mathbf{x}_t$ , representing the true locations of a turtle (longitude and latitude) at regularly spaced intervals,  $t$ , while the observed data,  $\mathbf{y}_{t,i}$ , consisted of locations recorded irregularly in time from satellite tags (the subscript  $i$  indexes multiple locations recorded during interval  $t$ ). In the second stage of our analysis, we used the framework developed by Morales et al. (2004) to model switches in movement behavior as a function of turtle size and environmental covariates, which we sampled for each estimated location  $\mathbf{x}_t$  (see *Oceanographic sampling*, below). The state variable,  $b_t$ , was a binary indicator of behavioral state, with the transition expression

$$b_t \sim \text{Bernoulli}(p_{b_{t-1}, \mathbf{z}_t}) \quad (1)$$

where  $p_{b_{t-1}, \mathbf{z}_t}$  was the probability of a turtle being in one of two unobservable behavioral states during interval  $t$ , and depended on the previous behavioral state ( $b_{t-1}$ ) and environmental covariates ( $\mathbf{z}_t$ ) sampled for location  $\mathbf{x}_t$ . We tentatively interpret states 1 and 2 as intensive-search or foraging vs. extensive-search or exploratory states, respectively (e.g., Fauchald and Tveraa 2003, 2006, Morales et al. 2004). Thus,

$$p_{1, \mathbf{z}_t} = \frac{\exp(\mathbf{z}_t \boldsymbol{\beta}_1)}{1 + \exp(\mathbf{z}_t \boldsymbol{\beta}_1)} \quad p_{2, \mathbf{z}_t} = \frac{\exp(\mathbf{z}_t \boldsymbol{\beta}_2)}{1 + \exp(\mathbf{z}_t \boldsymbol{\beta}_2)} \quad (2)$$

expressed the probability of a turtle being in state 1 at  $t$ , given that it was in state 1 or 2 at  $t - 1$ , respectively. Parameter vectors for each state ( $\boldsymbol{\beta}_1, \boldsymbol{\beta}_2$ ) were estimated from the data.

There were two observation equations for this state-space model: one for movement rates ( $d_t$ ; km/day) and one for turn angles ( $\theta_t$ ; radians), calculated from the locations ( $\mathbf{x}_t$ ) estimated during the first modeling stage. Data were viewed as random variables from distributions specific to each behavioral state. Following Morales et al. (2004), we assumed that turn angles came from wrapped Cauchy distributions, which are driven by two parameters that must be estimated: the mean turn angle ( $\varphi$ ) and the mean cosine of turn angles ( $\omega$ ). The density is

$$C(\theta) = \frac{1}{2\pi} \left[ \frac{1 - \omega^2}{1 + \omega^2 - 2\omega \cos(\theta - \varphi)} \right] \quad (3)$$

$$0 \leq \theta \leq 2\pi \quad 0 \leq \omega \leq 1.$$

For simplicity, and because we did not expect mean turn angle to be systematically different for the two behavioral states, we set mean turn angle ( $\varphi$ ) to zero. Thus, we only needed to estimate  $\omega$  for each behavioral state. In contrast to Morales et al. (2004), who used a Weibull distribution for movement rate, we assumed that movement rates for the two behavioral states came from normal distributions with parameters  $\mu$  and  $\sigma$ . Our principal reason for using a normal distribution was to always represent state 1 as the slower movement state

( $\mu_1 < \mu_2$ ). This constraint was easy to impose using the normal, but was difficult with the Weibull distribution in a hierarchical framework with multiple turtles. Movement rates were not close to zero, so we were not concerned that values from the normal distribution tails would be underrepresented in the data. Thus, for a given vector of behavioral states, the likelihood for our model was

$$P(\text{data} | \mu, \sigma, \omega) = \prod_{t=1}^T N(d_t | \mu_{b_t}, \sigma_{b_t}) C(\theta_t | \omega_{b_t}). \quad (4)$$

The ‘‘Jonsen method’’ also enables one to model switches in movement behavior, based on estimates for each behavioral state of mean turn angle and movement correlation parameters (Jonsen et al. 2005, 2007). However, we favored the ‘‘Morales method’’ because we felt that its constituent parameters—mean movement rate and variance in turn angles—offered a more biologically intuitive characterization of different behavioral types for our study species, and that the latter framework yielded a more believable separation of movement types when applied to the same loggerhead movement trajectory (see Supplement). Moreover, our desire to explicitly model behavioral switching as a function of environmental variables necessitated a two-stage modeling process because we needed location estimates from the Jonsen model before we could sample oceanographic data. Once we had location estimates and associated environmental data, the Morales framework was more conducive to modeling environment–behavior relationships. Jonsen et al. (2007) similarly evaluated the relationship between environment and behavioral state following output from their model that did not incorporate environmental covariates.

#### *Hierarchical Bayesian estimation*

We implemented both modeling stages in a hierarchical Bayesian framework, which enabled us to explicitly model individual heterogeneity in parameter estimates, and to make efficient use of data from all turtles, even those with few location data (e.g., Clark 2005, Jonsen et al. 2006). Turtle size was included as a binary fixed effect, with a value of 0 for turtles  $\leq 46$  cm curved carapace length (CCL;  $\sim 40$  cm straight carapace length [SCL]) and 1 for turtles  $\geq 53$  cm CCL (our data set did not include turtles between these values). This size break corresponds to the suggested transitional size between passive drifting and active habitat selection (Bolten 2003, Cardona et al. 2005). Random turtle effects were incorporated by estimating hyper-parameters, which describe population-level distributions and define the prior distributions of individual-level parameters (see Jonsen et al. [2006] for a flow chart of the hierarchical model structure). Thus, individual-level parameters were assumed to come from a normal (or in some cases beta) population-level distribution, or hyper-distribution (Table 1). We specified vague priors for hyper-distributions,

TABLE 1. Parameters and prior distributions for two stages of state-space modeling.

Parameter	Prior distribution	Interpretation
Stage-1 hyper-parameters		
$\theta_\mu$	uniform( $-\pi$ , $\pi$ )	mean turn angle for population
$\theta_\sigma$	uniform(0, 2)	SD of turn angles, due to individual heterogeneity
$\gamma_\mu$	beta(1, 1)	mean correlation in direction and turn angle between moves
$r$	half-norm(0, 1000)	shape parameter for the beta distribution for $\gamma_k$ (see below)
$s$	$= (r/\gamma_\mu) - r$	shape parameter for the beta distribution for $\gamma_k$ (see below)
Stage-1 parameters		
$\theta_k$	normal( $\theta_\mu$ , $\theta_\sigma^2$ )	mean turn angle for turtle $k$
$\gamma_k$	beta( $r$ , $s$ )	mean correlation between movements for turtle $k$
$\Psi_k$	uniform(0, 10)	a scaling factor that allows satellite tag error (Eq. 5) to vary for each turtle
$\Sigma$	Wishart	covariance matrix for process variance (Eq. 3); same for all turtles
Stage-2 hyper-parameters		
$\beta_{\mu,b,i}$	normal(0, 1000)	mean coefficient for covariate $i$ in state $b$ ; ( $i = 0, 1, 2, 3, 4$ )
$\beta_{\sigma,b,i}$	half-norm(0, 1000)	SD of coefficients, due to individual heterogeneity
$d_{\mu,b}$	half-norm(0, 1000)	mean movement rate in state $b$ , for population
$d_{\sigma,b}$	half-norm(0, 1000)	SD of movement rates in state $b$ , due to individual heterogeneity
$d'_{\mu,b}$	half-norm(0, 1000)	mean variance in movement rate for state $b$ , for population
$d'_{\sigma,b}$	half-norm(0, 1000)	SD of variance in movement rate, due to individual heterogeneity
$\omega_{\mu,b}$	beta(1, 1)	mean cosine of turn angles in state $b$ , for population
$r'_b$	half-norm(0, 1000)	shape parameter for the beta distribution for $\omega_{k,b}$ (see below)
$s'_b$	$= (r'_b/\omega_{\mu,b}) - r'_b$	shape parameter for the beta distribution for $\omega_{k,b}$ (see below)
Stage-2 parameters		
$\beta_{k,b,i}$	normal( $\beta_{\mu,b,i}$ , $\beta_{\sigma,b,i}^2$ )	coefficient for covariate $i$ , for turtle $k$ in state $b$
$d_{k,b}$	normal( $d_{\mu,b}$ , $d_{\sigma,b}^2$ )	mean movement rate of turtle $k$ in state $b$
$d'_{k,b}$	normal( $d'_{\mu,b}$ , $d'_{\sigma,b}^2$ )	SD of movement rate of turtle $k$ in state $b$
$\omega_{k,b}$	beta( $r'_b$ , $s'_b$ )	mean cosine of turn angles for turtle $k$ in state $b$

Notes: See Jonsen et al. (2005) for explanation of stage-1 parameters; see *Methods: State-space models* and Morales et al. (2004) for explanation of stage-2 parameters; also see Supplement for code.

consistent with prior specifications of Morales et al. (2004) and Jonsen et al. (2005, 2006). Some location estimates ( $\mathbf{x}_t$ ) did not have associated covariate estimates because the oceanographic variables we sampled were derived from satellite imagery whose quality is highly dependent on the amount of cloud cover in the region. We dealt with this by placing informative priors (normal[0,1]) on the missing covariates (covariates were standardized to normal[0,1] for analysis). We used Monte Carlo Markov chain (MCMC) methods in WinBUGS (version 1.4.1; Spiegelhalter et al. 2004) to implement our models. For the Jonsen model, we generated two MCMC chains, each with 20 000 iterations. We discarded the first 15 000 samples from each chain, and then thinned remaining observations by 10 to reduce autocorrelation within the samples. For Morales-based models, the chain length was 35 000. The first 10 000 were discarded and retained samples were thinned by 50. Thus, posterior distributions for each parameter were based on a total of 1000 independent samples.

#### Oceanographic sampling

We examined the possible importance of bathymetric depth, mean sea-level anomaly (MSLA), and the interaction of MSLA with turtle size as predictors of behavioral state. Previous analyses have shown that juvenile loggerheads in the western Mediterranean are generally associated with oceanic waters (>1400 m deep)

and seem to avoid waters of the continental shelf (<200 m; Cardona et al. 2005, Revelles et al. 2007). Polovina et al. (2004, 2006) described associations between some larger juvenile loggerheads and sea-surface heights, indicative of features such as upwellings, downwellings, or eddies that concentrate food resources (Rhines 2001, Jacobs et al. 2002). We sampled these variables for all locations along each turtle's estimated trajectory. The near real time (NRT) MSLA values (centimeters above or below average sea-surface height for that location) reflect ephemeral changes in surface height due to upwellings, gyres, or cyclonic eddies: indicators of surface productivity (Rhines 2001, Jacobs et al. 2002). MSLA data, produced by SSALTO/DUACS (Issue 1rev5) and obtained from Aviso (*available online*),<sup>6</sup> were available as 3–4 day composites, and had a spatial resolution of 0.25 degrees. We sampled bathymetric depth (m) from the S2004 1-min global grid (Marks and Smith 2006). This data set combines data from Smith and Sandwell (1997) and the General Bathymetric Chart of the Oceans (GEBCO) digital atlas (IOC, IHO, and BODC 2003). It employs the GEBCO data for high latitudes and longitudes, as well as in areas close to shore, while maintaining the power of the short-

<sup>6</sup> ([http://www.aviso.oceanobs.com/html/donnees/produits/hauteurs/global/msla\\_uk.html](http://www.aviso.oceanobs.com/html/donnees/produits/hauteurs/global/msla_uk.html))

TABLE 2. Information on 19 loggerhead sea turtles (*Caretta caretta*) and satellite transmitters deployed on these turtles in the western Mediterranean Sea.

Turtle ID	Size, CCL	Mass (kg)	Deployment date	Last transmission	No. days monitored	Transmitter model	Deployment longitude (°W)
Cc1	74.0	57.50	6 Jul 2004	12 May 2005	311	SDR-T16	5.44
Cc2	68.0	47.00	11 Jul 2004	30 Jul 2004	19	SDR-T16	5.19
Cc3	69.0	35.70	12 Jul 2004	14 Dec 2004	155	SDR-T16	5.17
Cc4	79.0	60.00	18 Jul 2004	3 Dec 2004	138	SPOT 4	4.87
Cc5†	60.5	31.60	19 Jul 2004	20 Jul 2004	1	SDR-T16	5.21
Cc6†	76.0	54.65	20 Jul 2004	28 Nov 2004	131	SDR-T16	5.22
Cc7†	76.0	55.00	22 Jul 2004	21 Dec 2004	152	SPOT 4	4.89
Cc8	30.0	4.50	20 Sep 2004	27 Mar 2005	188	SPOT 4	1.42
Cc9	71.0	40.00	10 Oct 2004	16 Oct 2004	7	SPOT 4	1.04
Cc10	32.0	5.80	13 Oct 2004	1 Nov 2004	19	SPOT 4	0.53
Cc11	26.0	2.80	24 Nov 2004	15 Mar 2005	111	SPOT 4	2.50
Cc12	53.0	NA	4 Dec 2004	18 Jun 2006	562	SPOT 4	1.04
Cc13	57.0	22.00	24 Jan 2005	13 Aug 2005	201	SPOT 4	2.93
Cc14	44.0	12.80	20 Mar 2005	16 May 2005	57	SPOT 4	2.00
Cc15	46.0	14.20	20 Mar 2005	9 Jul 2005	154	SPOT 4	2.00
Cc16	68.0	48.00	7 Jul 2005	21 Aug 2005	46	SPOT 4	4.55
Cc17	28.0	3.40	7 Jul 2005	30 Jul 2005	23	SPOT 4	4.58
Cc18†	74.0	54.00	12 Jul 2005	10 Jul 2006	363	SPOT 4	4.27
Cc19	77.0	54.00	9 Aug 2005	15 Oct 2005	67	SPOT 4	2.80

Note: Key to abbreviations: CCL = curved carapace length; NA = not available (turtle was not weighed).

† Four turtles were not used in state-space model analysis because they only transmitted location data for one day (Cc5) or left the Mediterranean and traveled across the Atlantic Ocean (Cc6, Cc7, and Cc18).

wavelength data in the Smith and Sandwell grid (Marks and Smith 2006).

#### *Propagating location uncertainty*

Estimating behavioral states under the Morales (2004) method assumes that animal locations, and hence rates and turn angles, are measured without error. However, location estimates from the Jonsen (2005) model are in fact described by posterior distributions that reflect location uncertainty. Because we believe that we should account for uncertainty in rates and turn angles (a function of location uncertainty) and location-specific environmental data when estimating state probabilities and effects of covariates, we conducted two sets of analyses: an initial one that included 15 turtles and did not address location uncertainty in estimating stage-2 model parameters, and a second analysis that included only nine turtles and addressed location uncertainty in stage-2 model estimates (see *Results: Movement behavior and oceanography: Analysis of 15 turtles ...* and *Analysis of nine turtles ...*, below). For the latter, we randomly selected 30 turtle pathways (location estimates from 30 MCMC sample sets) from the posterior distributions of location estimates from the stage-1 model. For each of the 30 trajectory sets, we sampled oceanographic data (depth and MSLA) and fit the stage-2 model. We appended the 1000 samples from each of the 30 stage-2 outputs to obtain a final posterior distribution (30 000 total samples) for stage-2 parameter estimates.

## RESULTS

### *Description of turtles and movement paths*

Nineteen juvenile loggerhead turtles (*Caretta caretta*) were captured, with sizes ranging from 26 to 79 cm curved

carapace length (CCL;  $57.0 \pm 18.9$  cm [mean  $\pm$  SD]) and from 2.8 to 60.0 kg ( $32.6 \pm 21.5$  kg [mean  $\pm$  SD]) (Table 2). Capture longitude and turtle sizes were significantly correlated (Pearson  $r = 0.56$ ,  $P < 0.05$ ), with larger turtles being caught further west (Table 2). Ten of the 11 turtles with CCL  $> 57.0$  cm (Table 2) were captured west of  $3^\circ\text{W}$  corresponding roughly to the eastern edge of the Alborán basin. All but one turtle (Cc17) with CCL  $\leq 57$  cm ( $n = 8$  turtles) were captured east of  $3^\circ\text{W}$  (Table 2). There was no relation between month of capture and turtle size (Pearson  $r = 0.13$ ,  $P > 0.05$ ). One turtle (Cc5) transmitted satellite data for only one day and was not considered in further analysis or interpretation. Monitoring duration of the remaining 18 turtles spanned 7–562 days ( $150.1 \pm 142.4$  days [mean  $\pm$  SD]; Table 2).

Of the 18 turtles with monitoring durations  $\geq 7$  days, post-capture movements exhibited two general patterns that seemed related to turtle size. Turtles with CCL  $\leq 57$  cm ( $n = 8$ ) (Cc8, Cc10, Cc11, Cc12, Cc13, Cc14, Cc15, and Cc17) gradually moved eastward through the Mediterranean Sea after capture (Fig. 2). Six (Cc8, Cc10, Cc13, Cc14, Cc15, and Cc17) of these eight smaller turtles spent most of their time in southern Balearic Sea (western Mediterranean basin); the other two small turtles (Cc11 and Cc12) moved along the Moroccan and Algerian coasts, apparently with the Algerian current, to more easterly basins. Turtle Cc11 moved into the Ionian Sea. Turtle Cc12 moved into the Tyrrhenian Sea before traveling north to the south coast of France and west along the Spanish coast (Fig. 2). The 10 turtles with CCL  $> 57$  cm displayed more variation in movement patterns. Three (Cc1, Cc3, and Cc4; Fig. 3) moved east across the Mediterranean in a manner similar to the smaller turtles, whereas seven (Cc2, Cc6,

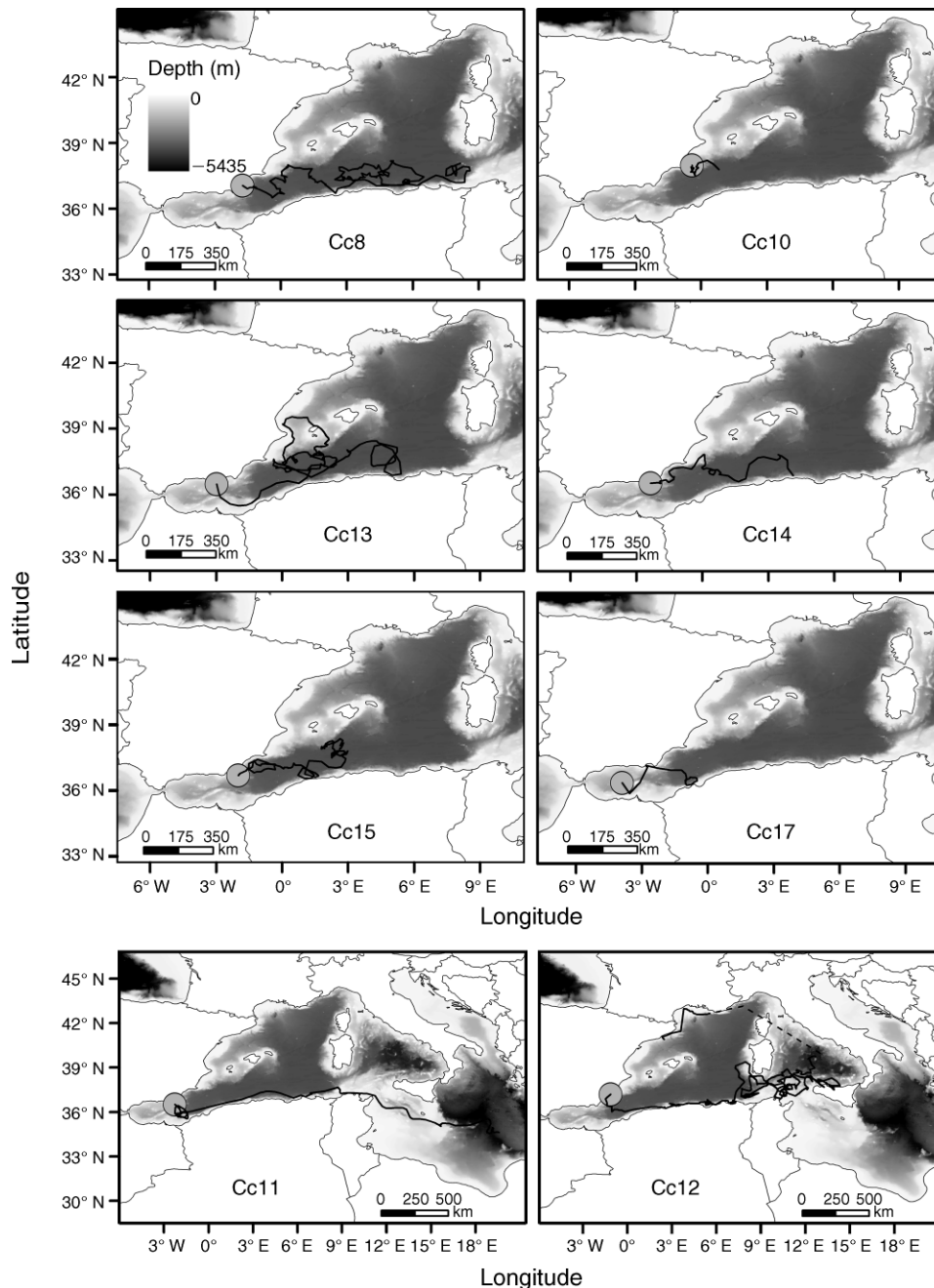


FIG. 2. Fitted trajectories from state-space models, based on Argos satellite telemetry data, of eight juvenile loggerhead sea turtles  $\leq 57$  cm CCL, captured in the southern Balearic Sea. The shaded circles at the west end of the trajectory indicate capture location. The dotted line for Cc12 represents a 37-day period (20 January–26 February 2006) during which no location data were recorded for this turtle.

Cc7, Cc9, Cc16, Cc18, and Cc19) were associated with waters of the Alborán Sea (see Plate 1). Three of these seven (Cc6, Cc7, and Cc18) left the Mediterranean and moved west across the Atlantic Ocean (Fig. 4). In the longest and most complete of these trans-Atlantic records (Cc18), the turtle traveled to the southern coast of Nicaragua in the Caribbean Sea (Fig. 4). Turtles Cc6

and Cc7 appeared to be moving toward the Caribbean and United States coast, respectively, before we stopped receiving transmissions.

#### *Movement behavior and oceanography*

The 15 turtles that remained in the Mediterranean Sea were considered for our state-space models. A total of

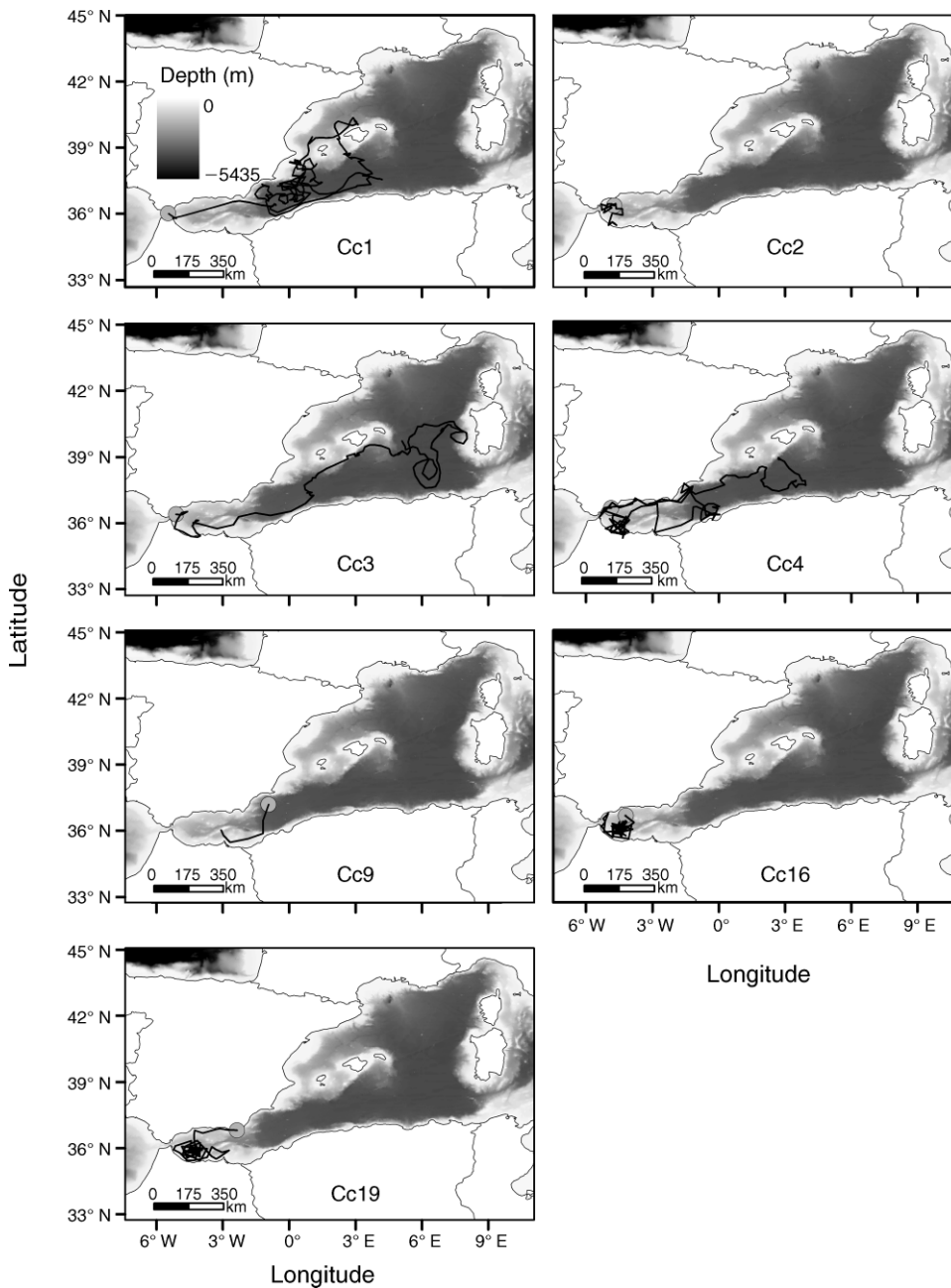


FIG. 3. Fitted trajectories from state-space models, based on Argos satellite telemetry data, of juvenile and subadult loggerhead sea turtles >57 cm CCL captured in the Alborán and Balearic Seas (western Mediterranean Sea) as monitored using Argos satellite telemetry. Circles indicate capture location.

5472 Argos-recorded locations from these turtles were entered into our analyses. At the time of this analysis the number of locations per turtle ranged from 38 to 728 locations (median: 359 locations). The locations spanned a total of 1861 intervals or “turtle-days,” with the number of days per turtle ranging from 7 to 410 days (median: 110 days). Stage-1 state-space models (see Supplement for parameter estimates) improved on unprocessed telemetry data by removing extreme loca-

tions and estimating more accurate trajectories than provided by unprocessed satellite tag data (Fig. 5).

*Analysis of 15 turtles in the western Mediterranean.*— We first describe population-level parameter estimates (hyper-parameters), based on the model that included 15 turtles and assumed that location estimates from the Jonsen model were error free. Mean movement rate of turtles in state 1 (intensive search) was 13.6 km/day (95% credible interval [CI]: 11.3–17.3 km), with an SD of



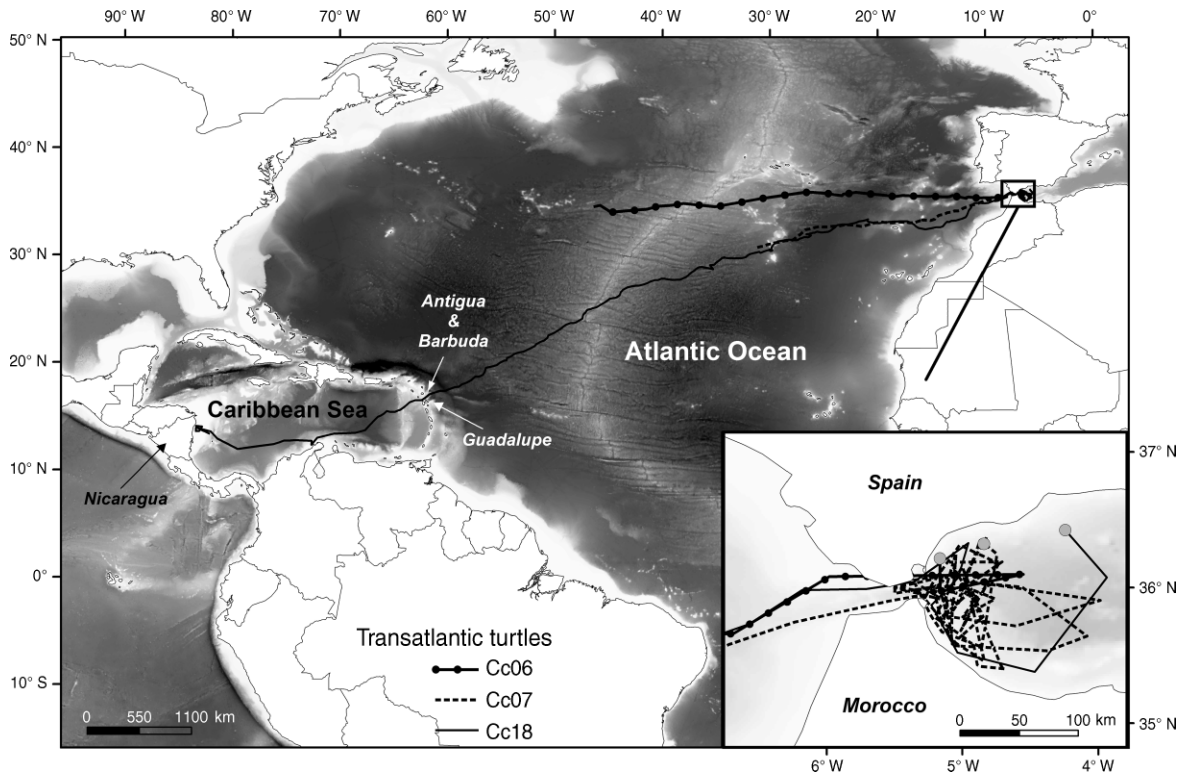


FIG. 4. Tracklines of three subadult loggerhead sea turtles as monitored using Argos satellite telemetry and processed using a Douglas filter (Douglas 2006). Turtles were captured in the Alborán Sea (western Mediterranean) and monitored for up to 363 days as they moved west across the Atlantic Ocean. The circles in the inset indicate capture location. Shading reflects bathymetry as in Fig. 1.

4.0 km (2.3–8.5 km) across individuals, compared to 37.8 km (31.4–43.8 km) with a SD of 10.2 km (6.9–15.6 km) across turtles in state 2 (exploratory). The wrapped Cauchy parameter,  $\omega$ , reflects the amount of variance in turn angles, with smaller values reflecting more tortuous movement. Median  $\omega$  for state 1 ( $\omega_{\mu,1}$ ) was 0.37 (95% CI: 0.28–0.46) compared to 0.44 (0.34–0.57) for state 2 ( $\omega_{\mu,2}$ ), which at first seems to suggest that movement tortuosity in slow (state 1) and fast (state 2) movement states was similar. However, tortuosity of state-2 movement varied considerably across individuals ( $\omega_{\sigma,2} = 0.30$ ; Fig. 6). For seven turtles (Cc1, Cc3, Cc8, Cc11, Cc12, Cc13, and Cc14)—all of whom traveled east through the Mediterranean following capture (Figs. 2 and 3)—the slower state was also more tortuous, as evidenced by non- or only slightly overlapping 95% credible intervals for the parameters  $\omega_{k,1}$  and  $\omega_{k,2}$  (Figs. 5A and 6). The opposite was true for four large turtles that used the Alborán (Cc2, Cc4, Cc16, and Cc19; Fig. 3); the faster state was highly tortuous for these turtles (Figs. 5B and 6). For four turtles (Cc9, Cc10, Cc15, and Cc17; Figs. 2 and 3), movement tortuosity was statistically similar for the two states (Fig. 6), but three of these turtles (Cc9, Cc10, and Cc17) had few location data ( $n = 7, 19,$  and  $23$  days, respectively; Table 2), and point estimates for all four of these turtles suggested

greater tortuosity in state 1. Thus, it appeared that state 1 (slower state) was typically more tortuous for turtles using oceanic waters east of the Alborán, and that movement characteristics outside of the Alborán Sea were distinctly different from movement within the shallower Alborán basins. The degree of certainty in assigning movement segments to one of the two behavioral states was generally high, with median  $\text{Prob}[\beta < 0]$  usually  $>0.75$  or  $<0.25$  (indicating state 2) (Fig. 5).

Coefficients describing effects of environmental features and turtle size on behavioral switching suggested that all covariates included in our model were important predictors of behavioral state. First, juvenile loggerheads were more likely to exhibit the slower state 1 (intensive search) movement when in deeper waters. Standardized hyper-parameters (denoted by subscript  $\mu$ ) for depth (subscript D), with subscript 1 or 2 indicating switching to state 1 from either respective state, were:  $\beta_{\mu,1,D} = -0.71$  (95% Bayesian CI =  $[-1.51, -0.13]$ ;  $\text{Prob}[\beta < 0] = 0.99$ );  $\beta_{\mu,2,D} = -0.37$  (95% CI =  $[-1.22, 0.13]$ ;  $\text{Prob}[\beta < 0] = 0.94$ ). Individual-level responses were generally consistent with this population-level result (Fig. 7). Second, juveniles of the larger size class showed more persistent bouts of “fast” swimming behavior, i.e., a larger turtle exhibiting state-2 movement was more

likely to remain in that state than was a smaller turtle. Standardized coefficients for turtle size (subscript S) were:  $\beta_{1,S} = -0.21$  (95% CI: [-1.37, 1.15];  $\text{Prob}[\beta < 0] = 0.64$ );  $\beta_{2,S} = -0.99$  (95% CI: [-2.54, 0.14];  $\text{Prob}[\beta < 0] = 0.95$ ). Finally, larger juveniles seemed to respond behaviorally to MSLA, with lower MSLA values increasing the probability of switching from fast (state 2) to slow (state 1) movement. Standardized hyper-parameters describing the effect of MSLA for larger juveniles (subscript MI) (i.e.,  $\beta_{\mu,i,MI} = \beta_{\mu,i,M} + \beta_{\mu,i,S \times M}$ , when size class = 1) were:  $\beta_{\mu,1,MI} = -0.15$  (95% Bayesian CI = [-0.92, 0.68];  $\text{Prob}[\beta < 0] = 0.65$ );  $\beta_{\mu,2,MI} = -0.56$  (95% CI = [-1.58, 0.07];  $\text{Prob}[\beta < 0] = 0.96$ ). Median and 95% credible estimates for the size  $\times$  MSLA interaction ( $S \times M$  subscript) terms themselves were:  $\beta_{\mu,1,S \times M} = -0.38$  (95% Bayesian CI = [-1.82, 0.86];  $\text{Prob}[\beta < 0] = 0.76$ );  $\beta_{\mu,2,S \times M} = -1.32$  (95% CI = [-3.18, 0.11];  $\text{Prob}[\beta < 0] = 0.97$ ). Smaller individuals did not seem to respond behaviorally to MSLA, with 28% and 12% of the posterior densities for  $\beta_{\mu,1,M}$  ( $\beta = 0.26$  [-0.64, 1.46]) and  $\beta_{\mu,2,M}$  ( $\beta = 0.74$  [-0.61, 2.26]) overlapping zero. After accounting for the role of turtle size, there did not appear to be any strong unique individual-level responses to MSLA (Fig. 7).

*Analysis of nine turtles in the Balearic Sea.*—Our first set of results suggested that it may not be appropriate to model movements in the Alborán Sea, Balearic Sea, and basins east of the Balearics as a single statistical population, since turtles using these areas displayed different types of movement. Therefore, we fit a separate stage-2 hierarchical model to the nine turtles that spent the majority of time in the southern Balearic Sea and did not move to more easterly basins (Cc1, Cc3, Cc4, Cc8, Cc10, Cc13, Cc14, Cc15, and Cc17; Figs. 2 and 3). This second set of analyses incorporated location uncertainty from the stage-1 Jonsen model, which varied considerably across turtles (Fig. 8), into stage-2 parameter estimation. Results were qualitatively similar to the analysis that included all 15 turtles, but with some noteworthy differences. Hyper-parameter estimates for mean movement rates were 16.0 (95% CI: 13.2–18.8) and 36.3 km/day (31.6–41.9), for states 1 and 2, respectively. These are similar to the first set of analyses; however variation across individuals was much lower in the second analysis, with a SD for the hyper-distribution of 2.9 km/day (1.1–5.5) and 3.1 km/day (1.5–7.2), respectively. Also, state 1 (slower) movement was definitively more tortuous in the newer model (hyper-parameters:  $\omega_{\mu,1} = 0.18$  [95% CI: 0.09–0.30];  $\omega_{\mu,2} = 0.44$  [0.30–0.58]), and tortuosity for state 2 also was less variable across individuals than in the previous model (Fig. 9). The exception to this was turtle Cc4, a large turtle (CCL = 79 cm), for which the faster mode was more tortuous. As in the first analysis, this contrasting result may be explained by fast tortuous movement displayed by Cc4 in the western Alborán Sea before it traveled into the southern Balearic Sea (Fig. 3).

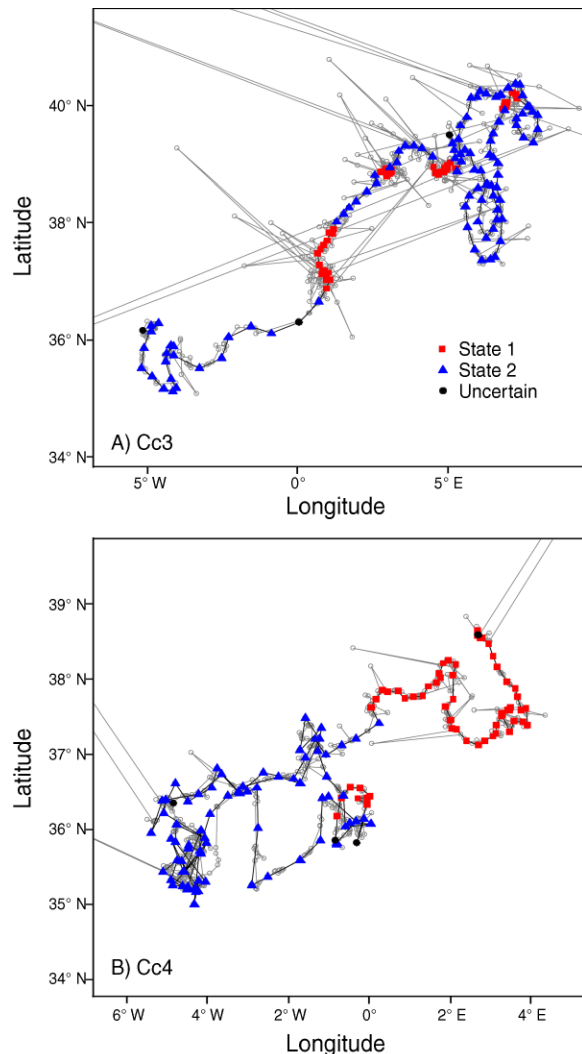


FIG. 5. Examples of using state-space models to fit movement trajectories to Argos data for juvenile loggerhead sea turtles in the western Mediterranean Sea. Gray lines and open circles depict location data from the Argos satellite system. Solid symbols depict estimated locations (at 1-day intervals) from stage-1 state-space models fit to the satellite-tag data, and estimated behaviors (uncertain, if  $\text{Prob}(\text{state } 1) > 0.25$  and  $< 0.75$ ) based on the stage-2 state-space model.

As in the first analysis, loggerheads in the southern Balearic Sea were more likely to exhibit intensive search behavior in deeper oceanic waters, as indicated by high probability that  $\beta_{\mu,1,D}$  and  $\beta_{\mu,2,D}$  differed from 0 (Table 3; also see Fig. 10). Also consistent with the first analysis, larger individuals seemed to respond behaviorally to MSLA. Standardized hyper-parameters describing the effect of MSLA for larger juveniles (i.e.,  $\beta_{\mu,i,MI} = \beta_{\mu,i,M} + \beta_{\mu,i,S \times M}$ , when size class = 1) suggested that the probability of  $\beta_{\mu,2,MI}$  being  $< 0$  was 0.97 (Table 3). Thus, lower MSLA values increased the probability of switching from fast (state 2) to slow (state 1) movement (Fig. 10A), but did not affect the probability

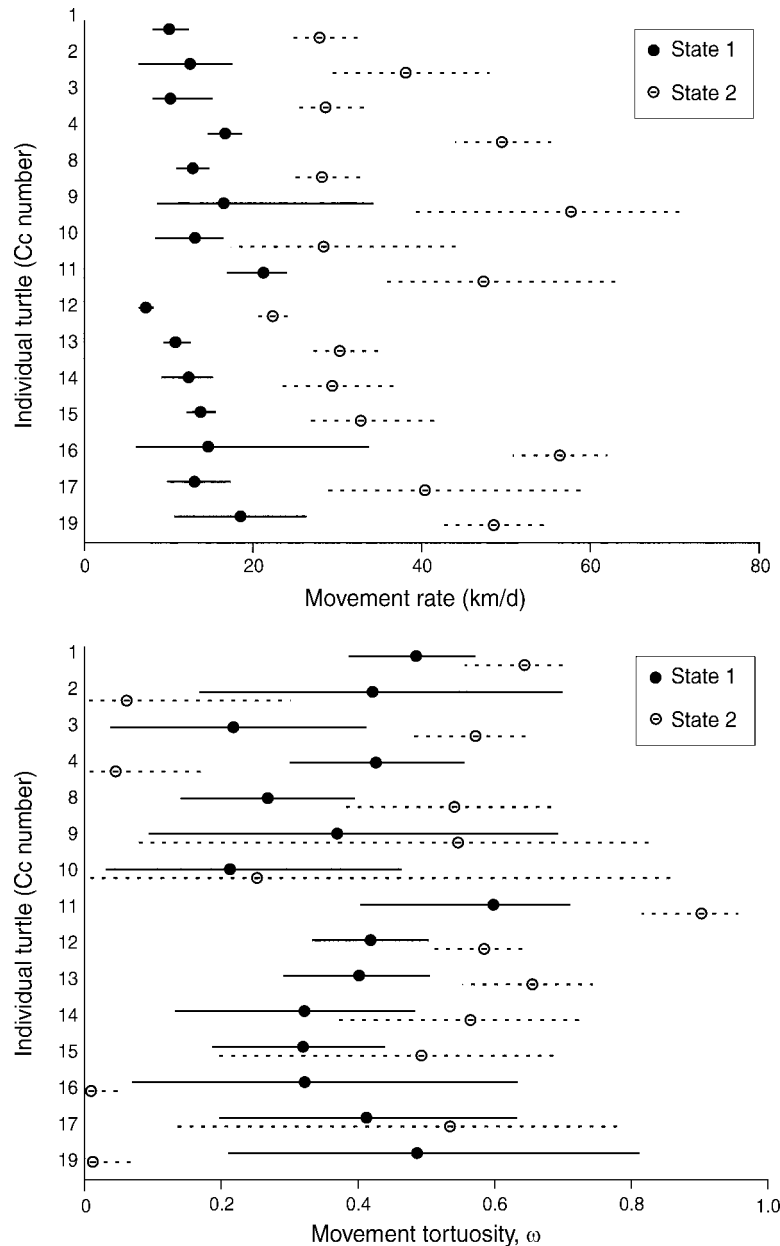


FIG. 6. Medians and 95% Bayesian credible intervals for standardized random-effect parameters describing mean movement rate and movement tortuosity to indicate the variance of turn angles (unitless, between 0 and 1; a wrapped Cauchy parameter, see *Methods: State-space models*) of two behavioral states, based on a stage-2 state-space model fitted to pathways of 15 juvenile loggerheads in the western Mediterranean Sea. Pathways estimated from the stage-1 state-space model were assumed to have negligible location error.

of staying in state 1 if already in that state. MSLA was not associated with behavioral switch probability for small individuals, with 16% and 31% of the posterior densities for  $\beta_{\mu,1,M}$  and  $\beta_{\mu,2,M}$  overlapping 0 (Table 3). Unlike the first-analysis results, size alone was not a strong predictor of behavioral state; larger juvenile turtles within the southern Balearic Sea did not conclusively display more persistent state-2 movement than smaller turtles ( $\text{Prob}[\beta_{1,S} < 0.32]$ ;  $\text{Prob}[\beta_{2,S} < 0] =$

0.83). As with the first analysis, there did not appear to be any unique individual responses to MSLA or depth apart from size-related responses to MSLA.

#### *Importance of propagating location uncertainty*

For comparison, we repeated our analysis for the nine turtles that used the southern Balearic Sea, but we treated location estimates from the stage-1 state-space model as error-free in the second stage of modeling (i.e.,

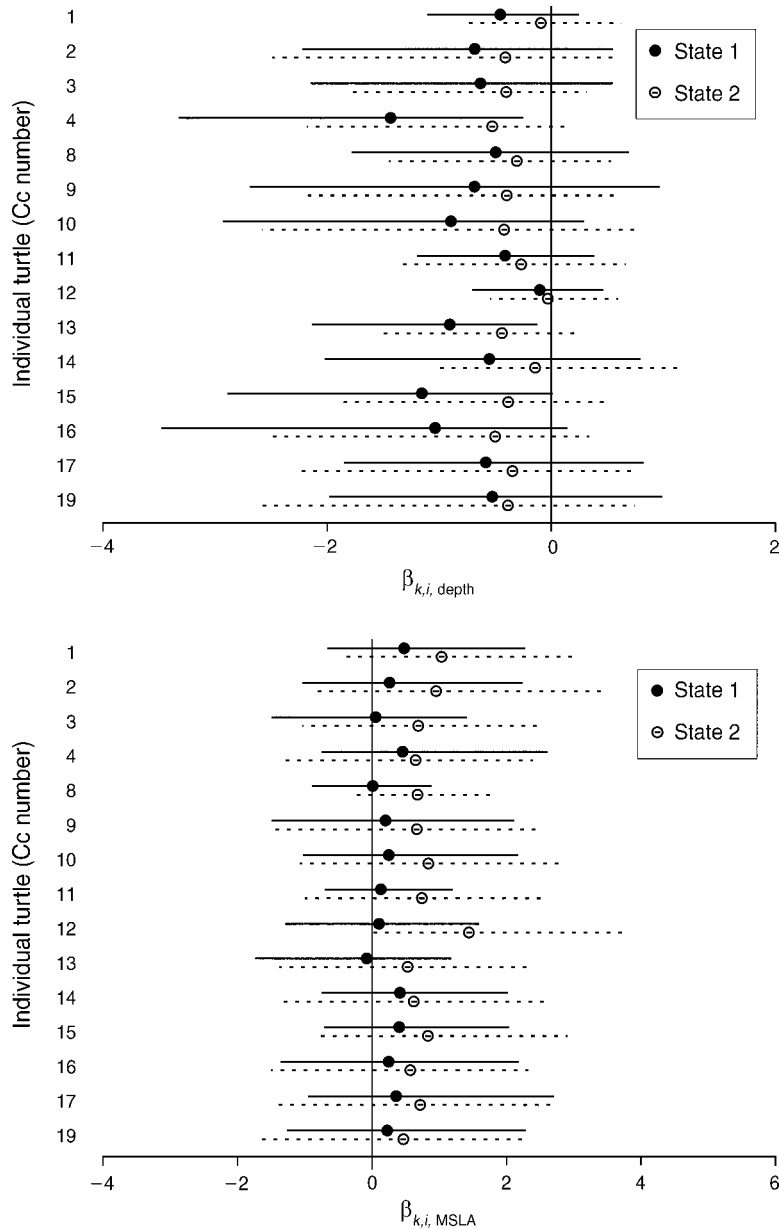


FIG. 7. Medians and 95% Bayesian credible intervals for standardized random-effect parameters describing the influence of depth and mean sea-level anomaly (MSLA) on behavioral switching by individual ( $k$ ) juvenile loggerheads, based on a stage-2 state-space model fitted to pathways of 15 turtles in the western Mediterranean Sea. Pathways were estimated from the stage-1 state-space model and were assumed to have negligible location error. Parameters indicate the effect of the variable on switching to state 1 from state  $i$ .

this was like our analysis of 15 turtles). This had minor but nontrivial impacts on our inference. Bayesian credible intervals for stage-2 parameters were wider when location uncertainty was addressed (Table 3), with consequences for interpreting the predictive importance of different parameters. For example, if we had ignored location uncertainty in our second analysis, we would have concluded a stronger effect of turtle size on the probability of switching from state 2 to state 1 (i.e.,  $\text{Prob}[\beta < 0] = 0.93$  when location uncertainty was ignored vs. 0.83 when location uncertainty was propa-

gated). Similarly, we may have inferred a meaningful impact of MSLA on behavioral switching in small turtles (which would have appeared opposite to that of large turtles) if location uncertainty was ignored.

DISCUSSION

*Size-dependent variation in distribution and movement*

Globally and across sea turtle species, few studies (Ferraroli et al. 2004, Polovina et al. 2004, 2006, Cardona et al. 2005, Revelles et al. 2007) have used

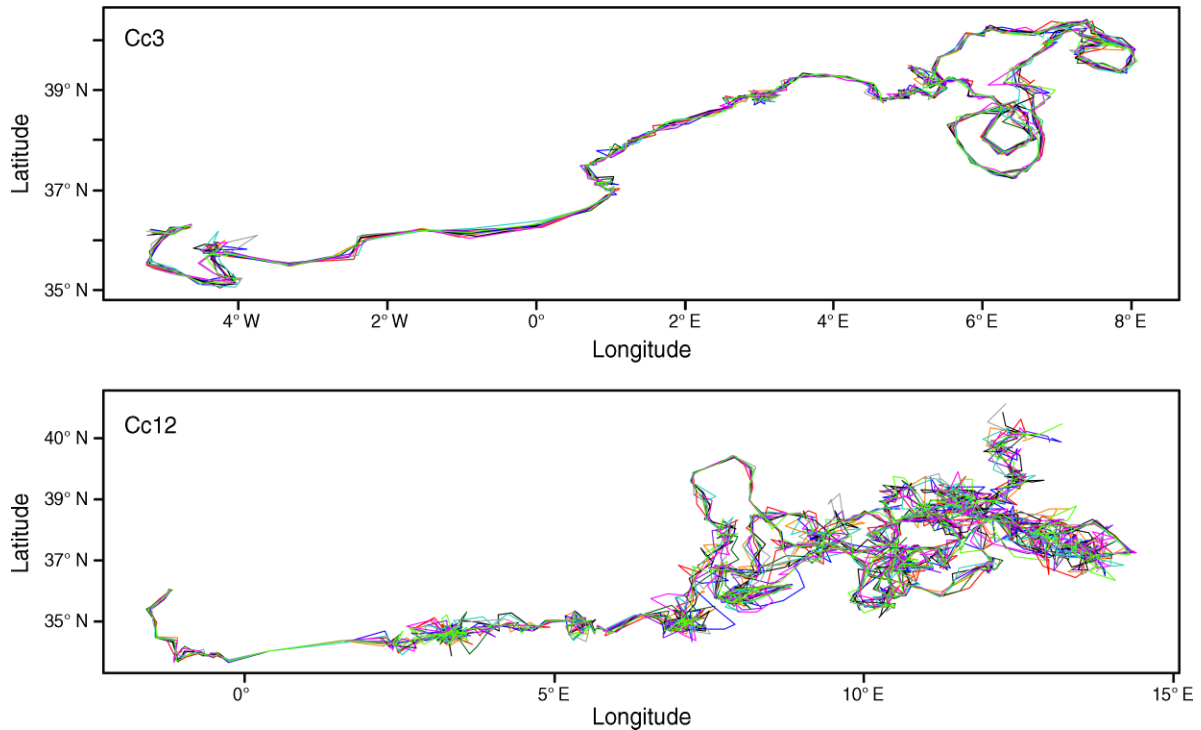


FIG. 8. Examples of location uncertainty in estimated pathways from stage-1 state-space models for two individual turtles. Each panel depicts 10 paths drawn from the posterior distributions for each location. These panels show how location uncertainty varies across individuals.

long-term movement data to describe pelagic habitat based on meso-scale oceanographic features, and fewer still (Jonsen et al. 2007) have done so using a robust analytical framework to address spatio-temporal autocorrelation in animal locations, location measurement error, individual heterogeneity in movement patterns, and behavioral heterogeneity within each trajectory. Failure to address individual heterogeneity in behavior can lead to difficulties in teasing apart population-level from individual-specific patterns, with consequences that include overemphasizing or underemphasizing the importance of environmental factors on animal movement. Because of the highly complex and variable movement patterns of loggerheads in our study (Figs. 2–4) and varying sample size across individuals, the use of hierarchical Bayesian state-space models was important for identifying both population-level descriptions and individual variation in the relationship between movement behavior and environmental features. Had we based our inference on separate analyses conducted for each turtle, we may not have identified any covariate effects on loggerhead movement behavior (Fig. 7).

Individual variation in loggerhead distribution appeared partially size dependent. With one exception (individual turtle [*Caretta caretta*] Cc17), only the largest turtles in our sample—those >57 cm CCL (curved carapace length)—were captured or spent time in the western Alborán Sea, and all turtles in this larger

class did so at some point. One possible explanation for this is that the western Alborán serves as a staging area for larger western Atlantic juveniles preparing to migrate to western Atlantic coastal areas. Why was the Alborán Sea not also used by smaller turtles in our study? One possibility is that strong east-bound currents originating from the narrow Straits of Gibraltar exclude smaller less-capable swimmers from the area. Evidence of current effects on movements was present in trajectories of animals that did use the Alborán; five of six turtles using this area exhibited fast yet highly tortuous movement, fundamentally different from movements in more easterly basins. Whether these erratic movements reflect foraging movements or the impact of currents on turtles intent on exiting the Mediterranean warrants additional study.

For individuals using the South Balearic Sea (finer scale), the importance of depth in our state-space models indicated that animals were more likely to switch to intensive-search (slower travel rate with higher turn angles [state 1] that we believe represents foraging behavior) when encountering deeper waters. Cardona et al. (2005) and Revelles et al. (2007) similarly observed many satellite-tagged turtles to select oceanic depths (>1400 m deep) or to avoid slope (200–1400 m) or shelf (<200 m) depths. Reasons for this are unclear, but presumably conditions in oceanic waters are more suitable to the feeding ecology of pre-neritic juveniles,

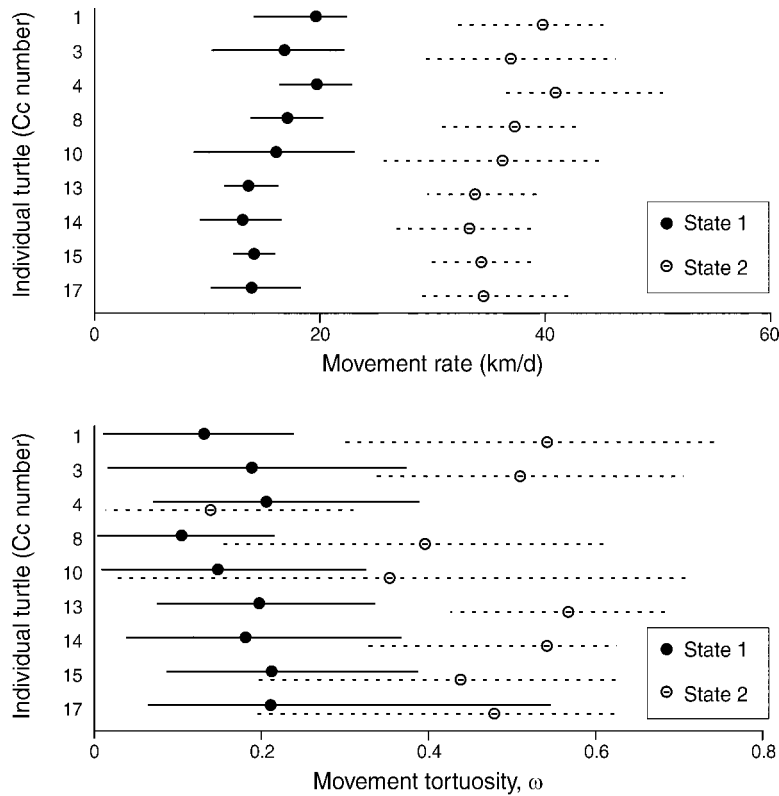


FIG. 9. Bayesian credible intervals for standardized random-effect parameters describing mean movement rate and movement tortuosity of two behavioral states, based on a stage-2 state-space model fitted to the pathways of nine juvenile loggerheads in the southern Balearic Sea. Parameter estimates account for location uncertainty from the stage-1 state-space model.

or oceanic waters may have lower predation risk (Walker 1994, Bolten 2003). The response of turtle movement to variations in sea-surface height (mean sea-level anomaly, MSLA) seemed to depend on the size of individuals. Larger pelagic-feeding juveniles (those  $\geq 46\text{cm}$  CCL) may be better able to respond to environmental features that concentrate prey resources (Cardona et al. 2005), either because their larger size enables them to better negotiate currents or because they

are more experienced at finding food. Or perhaps larger individuals have greater food requirements that necessitate use of high-quality feeding areas. Interestingly, MSLA was not a predictor of switching from state 1 to state 2 (faster travel rate, lower turn angles), only the other way around.

Our results seem consistent with the few previous studies that have related oceanic loggerhead movements to environmental features. We have already noted some

TABLE 3. Comparison of stage-2 state-space model parameter estimates.

Parameter ( $\beta$ subscripts)	Location uncertainty ignored			Location uncertainty propagated		
	Median	95% CI†	Prob( $\beta < 0$ )	Median	95% CI†	Prob( $\beta < 0$ )
Depth1 (D1)	-1.17	-2.31 to -0.24	0.99	-0.91	-2.34 to 0.45	0.93
Depth2 (D2)	-0.48	-1.88 to 0.30	0.91	-0.96	-2.71 to 0.26	0.94
MSLA1 (M1)	1.34	-0.49 to 2.80	0.07	1.05	-1.30 to 2.82	0.16
MSLA2 (M2)	1.04	-1.11 to 2.88	0.17	0.65	-2.20 to 2.77	0.31
Size1 (S1)	-0.37	-2.73 to 1.91	0.67	0.59	-2.25 to 3.72	0.32
Size2 (S2)	-1.24	-2.82 to 0.45	0.93	-1.30	-4.51 to 1.54	0.83
sizeMSLA1 (SM1)	-1.29	-3.16 to 0.96	0.90	-0.79	-3.15 to 2.24	0.75
sizeMSLA2 (SM2)	-1.61	-3.85 to 0.70	0.91	-1.87	-4.78 to 1.29	0.89
MSLA.lg1 (M11)	0.002	-1.02 to 1.24	0.50	0.22	-1.28 to 2.23	0.36
MSLA.lg2 (M12)	-0.54	-1.91 to 0.31	0.91	-1.15	-3.35 to 0.02	0.97

Notes: The estimates are based on satellite-tag data from nine juvenile loggerheads, when location uncertainty from the stage-1 model is ignored or included in the stage-2 analysis. Only fixed-effect and hyper-parameters are included here. Parameters indicate the effect of the variable on switching to state 1 from the suffix state (1 or 2).

† The 95% CIs are Bayesian credible intervals.

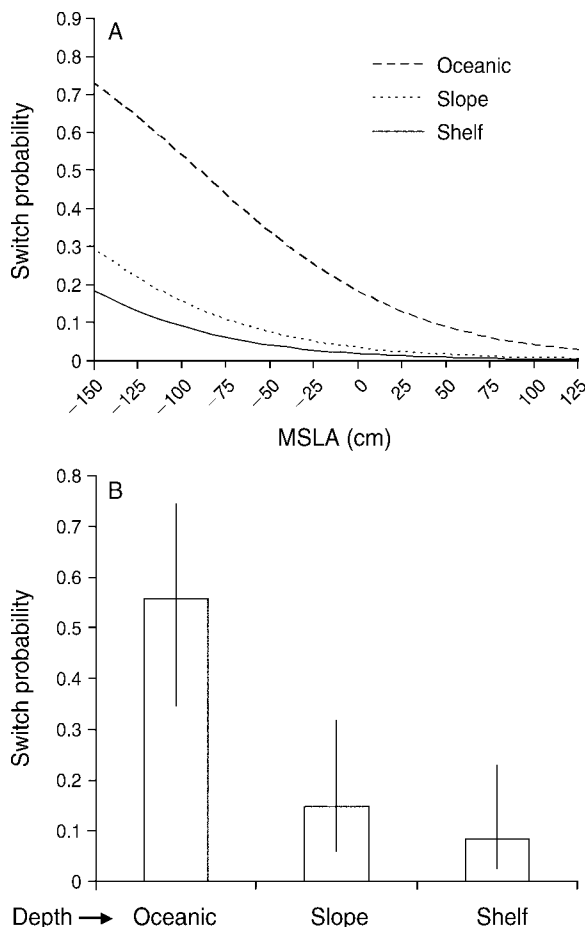


FIG. 10. Estimated probabilities of switching from behavioral state 2 (extensive search) to state 1 (intensive search) as a function of environmental covariates for turtles (A)  $\geq 53$  cm CCL and (B)  $\leq 46$  cm CCL. Estimates are based on a stage-2 state-space model of loggerheads in the Balearic Sea. Larger turtles switch as a function of mean sea-level anomaly (MSLA) and depth. Smaller turtles switch as a function of depth only. (A) Median probability estimates are shown across 95% of the range of sampled MSLA values, and at the median depth sampled within three categories: oceanic depth ( $< -1400$  m), continental slope ( $-1400$  to  $-200$  m), and continental shelf ( $> -200$  m). (B) Median switch probability (and 25th and 75th percentile) estimates are shown for the same depth values as in (A).

similarity between our results and those of Cardona et al. (2005) and Revelles et al. (2007) concerning a preference to utilize oceanic areas (vs. continental shelf or slope). However, in contrast with our results, those authors did not find differences in movement parameters as a function of turtle size or habitat type. The lack of size effect in their studies may have been due to a narrower range of turtle sizes included in each of their studies. Non-detection of habitat effects in their studies could possibly be explained by small sample size and examination of only small turtles (Cardona et al. 2005), or because analyses were conducted separately for individual turtles (as opposed to hierarchically), all of which spent very little time in non-oceanic bathymetry

domains and none of which occurred in the shallower and faster-moving waters of the Alborán Sea. That some larger juveniles in our study responded actively to locally depressed sea-surface heights is consistent with observations by Polovina et al. (2004, 2006), who described associations between some larger juvenile loggerheads and sea surface heights that were indicative of eddies in the North Pacific. Combining insights from their conclusions and ours, it seems that directed use of ephemeral or semi-permanent oceanic features that concentrate prey bases may be a strategy employed by larger oceanic juvenile loggerheads around the world. These results also may lend support to hypotheses for oceanic sea turtles in general, that large pelagic-feeding individuals respond actively to oceanographic features that concentrate resources (e.g., leatherbacks [*Dermochelys coriacea*]; Lutcavage 1996, Ferraroli et al. 2004, Eckert 2006).

Additional work is required to fully understand habitat selection and describe spatio-temporal patterns of juvenile loggerhead distribution in the Mediterranean. Spatial distributions of loggerheads may vary seasonally in the Mediterranean (Camiñas and de la Serna 1995; but see de Segura et al. 2006), and relationships between movement parameters and the environment may vary seasonally also. For model simplicity and for purposes of our analysis objectives, we elected to not run separate model sets for different seasons, or to include season-environment interaction terms. This would have reduced sample sizes too greatly for any particular analysis. We also did not undertake the complex task of modeling currents and their impact on movement in our framework, partly because currents data were not available at sufficient resolution at the time of our analysis, although currents undoubtedly play an important role for primarily passive drifting animals (Gaspar et al. 2006, Bentivenga et al. 2007). Future analyses should consider other variables that have been evaluated in studies of oceanic patchy-resource use, such as chlorophyll *a* values (Polovina et al. 2004, Pinaud and Weimerskirch 2005). Additional interactions or nonlinear relationships should also be explored. Finally, more work is required to improve interpretation of sea surface height data in our study as eddies or upwellings and to verify that these can be used as adequate surrogates of high food densities for turtles. Still, our analysis has helped advance the understanding of habitat selection and distribution of juvenile loggerheads in the western Mediterranean Sea, and has yielded important insight concerning the utility of different state-space model frameworks for understanding habitat selection through movement data in this and similar systems. Given the importance we found of propagating location uncertainty (from stage-1 model) in assessing environment-behavior relationships (stage-2 model), future research also should focus on developing a single robust framework that synthesizes the advantages of each framework we used, i.e., one that estimates true



PLATE 1. Juvenile loggerhead sea turtle, *Caretta caretta* (no. Cc6, 76.0 cm CCL) released with satellite transmitter in the Alborán Sea. This turtle was tracked for 131 days (Table 2), as it left the Mediterranean Sea and moved west across the Atlantic Ocean (Fig. 4). Photo credit: S. A. Eckert.

animal locations with uncertainty and incorporates the full characterization of that uncertainty (we used only 30 Monte Carlo Markov chain [MCMC] samples to characterize this) in a rate-angle-based estimation of behavioral states and the impact of environmental attributes thereon.

#### *New insights to loggerhead migration phenology*

In addition to inference based on analytical results discussed above, qualitative evaluation of our data provided new insight to larger-scale movements and distribution of loggerheads using the western Mediterranean Sea. First, we are the first to document real-time migrations of loggerheads from the Mediterranean across the Atlantic Ocean. Considering that at least one and possibly two of three tagged turtles that left the Mediterranean went to the Caribbean, we emphasize the possible importance of the Mediterranean Sea to western Atlantic nesting stocks south of the United States. Previous genetic analyses of western Mediterranean turtles have not adequately evaluated this. For example, Laurent et al. (1998) acknowledged that they did not consider haplotypes from nesting sites south of the United States. Carreras et al. (2006) did include haplotypes from Mexico and Dry Tortugas but not other Caribbean or Latin American sites. These authors identified disproportionately large genetic contributions

from Dry Tortugas and Mexico to some foraging areas in the Mediterranean, Azores and Madeira, and they noted that at least 2.7% (13 of 478) of their sampled turtles may have come from nesting populations not considered in their study. Although this is a small fraction of animals using the Mediterranean, these individuals could constitute significant portions of small nesting populations in Latin American or Caribbean countries. Understanding source populations throughout the Mediterranean requires sampling a majority of subbasins (Carreras et al. 2006), yet genetic sampling with consideration of Caribbean or Latin American nesting populations has not been conducted in areas used by our study turtles (Alborán and southern Balearic Seas).

Turtles in our sample that left the Mediterranean for the western Atlantic (74–76 cm CCL) are the largest loggerheads recorded in the Mediterranean that are presumably of western Atlantic origin. Laurent et al. (1998) suggested that loggerheads from western Atlantic stock leave the Mediterranean well before attaining these sizes, which correspond to those of neritic-stage residents in western Atlantic coastal waters (Bolten 2003). It therefore seems that larger western Atlantic juvenile loggerheads in the western Mediterranean may delay trans-Atlantic movement to take advantage of abundant food resources in the Alborán Sea. Loggerheads apparently feed in large seasonal rafts of sardine



crab (*Polybius henslowii*) off the northwest coast of Morocco (A. G. de los Ríos [Museo del Mar, Departamento de Biología, Ceuta, Spain], *personal communication*). Moreover, Tomás et al. (2001) found that fishes, mostly likely discarded bycatch from fisheries operations, were the most important prey group for western Mediterranean loggerheads of all size classes (34–69 cm CCL). Therefore, opportunistic loggerheads may be exploiting a relatively new and potentially superabundant food resource. An alternative explanation for our observation of large western Atlantic juveniles in the Alborán Sea is that these individuals had already completed a first east-west trans-Atlantic crossing and then re-entered an oceanic existence (and the Mediterranean) for a second time. Such a developmental remigration was documented for a 78-cm loggerhead subadult captured in the Cape Canaveral ship channel in Florida and later recaptured near the Azores Islands (Eckert and Martins 1989).

The occurrence of large turtles in the Alborán allows for the possibility that subadult loggerheads from western Atlantic stocks are using neritic habitats within the Mediterranean, in contrast with previous conclusions (Laurent et al. 1998, Margaritoulis et al. 2003). Additional studies of loggerhead behavior and diet in this region are needed to resolve this question, but given these turtles' large sizes, benthic feeding in this area seems possible (Bjorndal et al. 2000, Bolten 2003). If so, then western Atlantic loggerheads may be shifting to a partially neritic lifestyle prior to their trans-Atlantic move to western Atlantic coastal habitats. Alternatively, if western Atlantic turtles are not beginning to use benthic habitats in the Mediterranean, then turtles in our sample are among the largest oceanic-stage loggerheads recorded for the western Atlantic population (Bjorndal et al. 2000, Bolten 2003). Either way, our data challenge conventional assumptions about size-dependent migration phenology of western Atlantic loggerheads using the Mediterranean Sea, adding evidence to suggestions that the developmental migration of this species is complex and plastic, with multiple shifts between neritic and oceanic lifestyles and multiple circumnavigations of the Atlantic Ocean (Bolten 2003). Addressing these hypotheses should become an area of active research.

Finally, there are important conservation implications of documenting use of the western Mediterranean by large turtles (e.g., 68–79 cm; Table 2). A size of 74 cm CCL corresponds roughly to the cusp of "small neritic" and "large neritic" stages defined for population models of Atlantic nesting loggerheads (Heppell et al. 2003). Survival rates of juveniles in these larger size classes has an especially large impact on population-growth projections for western Atlantic loggerheads (Crowder et al. 1994, Heppell et al. 2003). It therefore appears that conservation measures to reduce bycatch in the western Alborán Sea would be particularly beneficial to recovery of Atlantic loggerhead populations.

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#### SUPPLEMENT

WinBUGS code, and sample data and initial values, for stage-2 state-space model analysis of movement paths (*Ecological Archives* A018-007-S1).