Changepoint analysis: a new approach for revealing animal movements and behaviors from satellite telemetry data

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Abstract. While telemetry is an invaluable tool for tracking animal movement patterns, the data generated by this technique is often challenging to interpret. Here, we addressed this issue by developing a novel method, based on changepoint analysis, which incorporated both the horizontal and vertical movement metrics and compared this output to that from a switching state-space model (SSSM) that categorized behavior based on horizontal movement metrics. We deployed 20 satellite transmitters on postnesting loggerhead turtles at Rethymno, Crete, Greece between 2010 and 2011 to monitor their at-sea behavior. We used both models to identify behavioral changes, such as the switches from migration to foraging, and from foraging to overwintering. The satellite-tracked turtles exhibited three discrete migratory strategies, with 9 turtles migrating southwards to the coast of northern Africa, 6 turtles migrating northwards into the Aegean Sea, and 4 turtles remaining resident in the waters of Crete. The SSSM readily identified the switch from transiting to ARS behavior in most animals, but the CPA model was able to distinguish multiple modes and more subtle shifts in behavior corresponding with shifts from migration to foraging to overwintering behaviors. We have shown that by incorporating vertical movement metrics into the analysis of telemetry data, previously hidden shifts in behavior can be revealed. The resulting increase in ability to discern complex behavioral patterns of animals remotely will likely yield better management and conservation decisions for a wide array of organisms.

Key words: Aegean Sea; Caretta caretta; Crete; foraging; Gulf of Gabès; loggerhead sea turtle; Mediterranean Sea; migration; overwintering; switching state-space model.

INTRODUCTION

Identifying the behavioral states of animals from satellite telemetry data is becoming increasingly common as new statistical approaches are developed (Jonsen et al. 2013). However, rarely do these approaches account for the full suite of data available through modern satellite telemetry
devices (Bestley et al. 2013, 2015). A common approach for discerning different behavioral states from satellite telemetry data is to use a switching state-space model (SSSM; Jonsen et al. 2005). SSSM identifies a switch between two behaviors: transiting, which is characterized by movement at high rate and low turn angle; and area restricted search, which is characterized by localized movement of low rate and high turn angle (Bailey et al. 2009). However, using SSSM based on horizontal metrics alone is not universally applicable to all species, as some species may forage while exhibiting wandering movements (Hays et al. 2006), and residential movements do not always correspond to foraging (Bestley et al. 2015).

Due to the computational complexities of expanding state-space models (SSM) to incorporate more variables beyond turn angle and rate, limited work has been done to include additional metrics available through telemetry systems (Jonsen et al. 2013, but see Bestley et al. 2013, 2015). SSM requires a predetermined scale to be incorporated into the model to identify the specific behaviors (Jonsen et al. 2005). As a result, thresholds must be determined prior to running the SSM to calculate a change in behavior (Bailey et al. 2008). This becomes complicated when not all behaviors are known or not enough information about known behaviors exists to create thresholds within the various available metrics (Bestley et al. 2015). We developed a model, based on the changepoint method (Killick and Eckley 2014), that identifies change in multiple horizontal and vertical movement metrics simultaneously without the prerequisite of determining thresholds.

Changepoint analysis (CPA) is a tool used to estimate a point change in the mean and/or variance of time-series data (Killick and Eckley 2014). CPA has been used in a variety of fields ranging from finance (Zeileis et al. 2010) to oceanography (Killick et al. 2010). Currently, the most common search method to find changepoints is binary segmentation (Killick and Eckley 2014). To find changepoints, binary segmentation first splits the data into two segments based on user decided statistical properties. This step is then repeated on the two new segments, and if a changepoint is identified within the segments, then they are split further. This process continues until no more changepoints are found. Since CPA was not developed for a unique data type, it is very flexible in its applications, with the simple assumption that the data are in chronological order (Killick and Eckley 2014). This flexibility allowed us to develop a model, incorporating CPA, using the full suite of data available through modern telemetry systems.

We focused our research on the third largest nesting population of loggerheads in Greece, located at Rethymno, Crete (Margaritoulis et al. 2003, 2009). Previous tracking of loggerheads in the Mediterranean show they migrate in roughly straight lines to their foraging locations where they take up residence (Schofield et al. 2013, Hays et al. 2014). As these movement patterns fit closely with the assumptions that area restricted search is linked to foraging, these data should be readily interpretable using SSSM. Typically these turtles exhibited a transiting behavior of directed movement away from the nesting beach, followed by area restricted search behavior upon arrival at foraging grounds (Schofield et al. 2013). However, not all turtles exhibited a postnesting migration and at the foraging grounds, turtles have been documented exhibiting overwintering, which involves long periods of inactivity and very long dive durations, in addition to foraging (Hochscheid et al. 2005, 2007, Broderick et al. 2007). As a result, with the range of potential behaviors that exist for this population, developing a model to account for this variety is essential. An analysis combining horizontal and vertical movement data may provide a clear picture and reveal more precisely how these turtles make use of the Mediterranean Sea.

Here we present the first use of CPA to investigate the at-sea behavior of sea turtles. We incorporated nine movement metrics, calculated from the satellite transmitter data from 19 loggerheads, into the CPA model to identify the behavioral states of loggerheads at-sea. We also used SSSM to analyze the raw telemetry data and determine behavioral modes for each turtle. When possible, we compared the results from the SSSM and the CPA to identify the similarities and differences between our model and the most commonly used method to determine animal behavior from satellite transmitters.
METHODS

During 2010 and 2011, we deployed 20 satellite transmitters on adult female loggerhead turtles that were encountered opportunistically during nightly patrols of Rethymno beach (latitude 35.385°, longitude 24.590°). Those sections of beach have historically been patrolled by the Greek sea turtle conservation organization ARCHELON, and were observed to have the highest density of nesting activity in that region.

Satellite transmitter configuration

We used Wildlife Computers’ (Redmond, Washington, USA) tag models Mk10-PAT for 19 turtles and Mk10-AF (with Fastloc GPS capabilities) for 1 individual. The satellite transmitters were attached based on methods described in Patel (2013). We obtained location, dive, and temperature data, taking advantage of the PAT tags’ capabilities for opportunistic transmissions as the turtles swam. To prolong battery life, in 2010, we set the transmitters to a 6 hour on: off duty cycle, with a maximum of 75 transmissions per day, with unused transmits carried over to the next day. For the 2011 season, we programmed the transmitters with a 24 hour duty cycle with the overall number of transmissions limited to 52 per day. All transmitters sampled and summarized diving data (dive depth, dive duration, and time at depth) in pre-assigned bins. A dive was classified as a movement deeper than 1 m and lasting longer than 1 minute. The histogram bins for dive depth and time at depth were 5, 10, 15, 20, 25, 30, 35, 40, 45, 50, 75, 100, 200 and >200 m of depth. Dive durations were placed into bins of 2, 5, 10, 20, 30, 40, 50, 60, 90 and >90 minutes. In addition, maximum and minimum temperatures were recorded at the sea surface and at intervals of depths of 8 m. The transmitters were programmed to compile and transmit dive and temperature data, formatted as histograms summarizing 4-hour periods.

Postnesting movements and behaviors

We conducted all mapping and plotting of spatially referenced data using ArcGIS 10.2 (ESRI 2011). We determined the start of postnesting behavior as the time after ultrasonography revealed an empty ovary (Patel et al. 2015), or by receiving successive locations as the turtle was obviously moving away from the nesting beach.

Switching state-space model (SSSM)

To generate daily position estimates at evenly spaced time intervals from irregular satellite locations, we applied a Bayesian switching state-space model (Jonsen et al. 2007, Bailey et al. 2008) to all raw location data, Argos LC 3 – B, for each track (n = 19). Location estimates were inferred by coupling a statistical model of the observation method (measurement equation) with a model of the movement dynamics (transition equation; Patterson et al. 2008). The measurement equation accounted for errors in observed satellite locations (Vincent et al. 2002). When satellite positions were missing, linearly interpolated positions were used as initial values (Bailey et al. 2008). The transition equation was based on a first-difference correlated random walk model.

For each of two behavioral modes, behavioral mode 1 was considered to represent transiting behavior (e.g., migration) and behavioral mode 2 represented area-restricted search behavior (e.g., foraging, breeding and overwintering; Bailey et al. 2009). Transiting was characterized by having a turn angle of closer to 0 with autocorrelation higher than during area-restricted search (Jonsen et al. 2007). Calculated values of <1.25 were categorized as behavioral mode 1, while those >1.75 were considered behavioral mode 2. All values in-between were regarded as uncertain behavioral mode (Jonsen et al. 2007, Bailey et al. 2012).

The model was fitted using the R software package (R Core Team 2014) and Winbugs software (Lunn et al. 2000). Two chains were run in parallel, each for a total of 30,000 Markov Chain Monte Carlo Samples, with the first 10,000 samples discarded as burn-in, and the remaining samples thinned, retaining every fifth sample to reduce autocorrelation (Blanco et al. 2012).

Changepoint analysis (CPA)

One of our primary objectives was to expand on analysis techniques for telemetry data, beyond merely analyzing location or distinguishing between two behavioral states. To accomplish this, we took advantage of the full suite of metrics provided by the transmitters and incorporated many horizontal and vertical movement...
data for each turtle into a series of changepoint analyses. The model was run using the changepoint package for R with binary segmentation (Killick et al. 2012, Killick and Eckley 2014). To more fully interpret the at-sea behavior of these turtles, we used a total of 9 separate measured variables that we could detect remotely. These were turn angle and rate of travel, percentage of time at surface (above 5 m of depth), percentage of time above median dive depth for that period, mean number of dives, max dive depth, mean dive duration, max dive duration, and variance in dive duration. The two horizontal movement metrics, were calculated by feeding raw location data from ARGOS into algorithms and script we generated using dBase Plus. To account for Argos location error, we filtered locations when the rate exceeded 50 km day\(^{-1}\), and recalculated rate and turn angle until we returned no rates exceeding 50 km day\(^{-1}\) (Freitas et al. 2008, Lowther et al. 2015). We chose 50 km day\(^{-1}\) as the upper limit threshold as Schofield et al. (2010) found loggerheads in the Eastern Mediterranean migrate at a mean (± SD) rate of 1.5 ± 0.57 km h\(^{-1}\).

Using the changepoint analysis we calculated when any shift in the mean and variance within each behavioral parameter occurred. For each selected metric, we calculated a maximum of 20 changepoints, well above the number of actual distinct behavioral modes we would expect for a sea turtle. The changepoints for each turtle were then ranked to reflect the relative strength of the detected shift. Since changepoints are calculated along a timeline, when the 9 parameters were aligned we could determine at which dates and times there were discrete shifts in many behavioral metrics simultaneously. When there were simultaneous shifts (within a day) in several metrics, it was deemed that an individual turtle had undergone a major change in at-sea behavior. We associated the calculated behaviors with common sea turtle postnesting behaviors of migration, foraging and overwintering, based on chronological order, and previous assessments of each (Godley et al. 2003, Broderick et al. 2007). We deemed the other behaviors (n = 2) as transitional between the common behaviors due to the short duration of each, along with the chronology.

Combining the two analytical methods, we used results from both the switching state-space model and the changepoint analyses to determine the dates and locations of shifts and occurrence of various at-sea behaviors, such as migration, foraging and overwintering, and to characterize the movement and dive patterns associated with each major behavioral mode. In addition, we compared dive behavior of each turtle for foraging and overwintering, as well as the location of residency in the Mediterranean. For statistical comparisons, we performed one-way ANOVAs with a statistical significance at a level of 0.05. Statistical analyses were performed in R (R Core Team 2014).

**RESULTS**

We successfully tracked 19 of the 20 tagged turtles as they moved away from the beaches after nesting in Rethymno during the two years of study. In all, the tracking durations during postnesting periods ranged from 11 to 250 days (mean ± SD: 136 ± 74.3 days), making a cumulative total of 2718 turtle days of tracking data. Five transmitters from 2010 averaged 104 ± 68.3 days, while the 15 transmitters from 2011 with the updated duty cycle averaged 147 ± 75.2 days. We received a total of 4066 location points along with dive behavior histograms for 2601 four-hour time periods and temperature histograms for 1065 separate periods.

After completing nesting for the season, four turtles remained in the coastal waters of Crete for the remainder of their tracking durations, which ranged from 171 to 250 days. Three of these turtles resided at separate sites along the north coast of Crete and the fourth moved to the island of Gavdos, 35 km south of Crete. Migration distances for the 15 turtles that traveled away from Crete, as calculated using the unfiltered raw Argos satellite data, ranged from 237 to 2347 km, traveling at speeds ranging from 36.0 to 52.8 km per day. Nine individuals traveled to the northern African coast, with 8 ultimately settling in the Gulf of Gabès region of Tunisia, and 1 apparently establishing residency along the northeastern Libyan coast. The remaining six turtles that migrated, traveled north into the Aegean Sea. Two traveled to the Saronikos Gulf, near Athens; two turtles apparently established residency near the central Aegean islands, Ikaria and Naxos; and two migrated to the coastal waters of Turkey
near Izmir and Bodrum.

Switching state-space model analysis

Using the switching state-space model to analyze horizontal movement patterns, we were able to distinguish two separate modes of behavior from the modeled location data: behavior mode 1 (transiting), and behavior mode 2 (area-restricted search; Table 1; Figs. 1 and 2). Combining all 2712 daily modeled data points for all turtles, we estimated that collectively turtles spent 11.4% of the time in behavior mode 1, and 76.3% of the time in behavior mode 2, with the remaining 12.3% calculated as uncertain behavior (1.25 < bmode value < 1.75).

When viewed individually, the SSSM analysis designated that 14 of the 15 turtles that migrated away from Crete exhibited behavior mode 1 for some portion of their time at sea. While turtles were in this transiting mode, calculated rates of travel ranged from 32.5 to 53.6 km per day (mean ± 27.5 ± 6.0). The individuals that traveled to the

Table 1. Summary data of results from the SSSM and CPA analyses.

| Mode and description | Turtles (n) | Aegean Sea | North African | Cretan resident | % total time | No. days | Travel rate (km/day) | No. dives | Dive duration | % time above 5 m |
|----------------------|------------|------------|---------------|-----------------|-------------|----------|----------------------|-----------|---------------|-----------------|
| SSSM behavioral modes|            |            |               |                 |             |          |                      |           |               |                 |
| B1, transiting       | 6          | 8          | 0             | 11.40           | 24.3 ± 19.1 | 27.5 ± 5.96 | 11.4 ± 7.7          | 18.5 ± 17.4 | 55.80         |
| B2, area restricted search | 5        | 6          | 4             | 76.30           | 132.9 ± 19.2 | 11.3 ± 3.05 | 10.6 ± 9.6          | 18.6 ± 20.0 | 30.40         |
| CPA behavioral modes |            |            |               |                 |             |          |                      |           |               |                 |
| CP1, migration       | 6          | 9          | 0             | 19.20           | 36.2 ± 12.9 | 23.0 ± 8.93 | 14.1 ± 8.7          | 16.0 ± 14.9 | 52.30         |
| CP2, foraging        | 5          | 8          | 4             | 45.80           | 70.3 ± 33.0 | 10.7 ± 2.74 | 11.2 ± 9.8          | 19.1 ± 18.5 | 32.00         |
| CP3, overwintering   | 2          | 3          | 3             | 21.30           | 71.9 ± 38.2 | 7.36 ± 1.89 | 2.2 ± 2.6           | 64.1 ± 40.7 | 11.00         |
| T1–2, transition 1–2 | 4          | 7          | 3             | 10.70           | 20.8 ± 10.8 | 15.6 ± 4.95 | 12.5 ± 8.9          | 16.6 ± 15.6 | 44.70         |
| T2–3, transition 2–3 | 0          | 1          | 1             | 3.03            | 41.0 ± 8.48 | 12.9 ± 1.48 | 12.7 ± 15.7         | 16.6 ± 19.7 | 21.20         |

Note: Results show mean ± SD.

Fig. 1. Results from the SSSM for the 15 loggerhead turtles that migrated away from Crete. Each track line is colored to represent a different turtle and each circle represents a daily location estimate from the SSSM. The circles are colored based on the inferred behavior mode at each location.
African coast spent a mean of 33.8 days (SD ± 9.3) in transiting mode, compared to those that ultimately settled in the Aegean who only spent a mean of only 7.7 days (SD ± 2.3) transiting. According to the SSSM analysis, two individuals that migrated to Tunisian waters, turtles 1 and 8, only exhibited behavior mode 1, even though both turtles clearly stopped migrating after they reached the Gulf of Gabès region. For turtle 2, on the other hand, the SSSM calculated that it only exhibited uncertain behavior throughout the tracking duration; while it also clearly exhibited a directed migration towards Tunisia.

During transiting behavior, as calculated by the SSSM, turtles (n = 14) averaged (mean ± SD) 11.4 ± 7.7 dives per four hour sample period, with 55.8% of dive time spent between 1 and 5 m of depth. Dive durations during SSSM behavior mode 1 averaged 18.5 ± 17.3 minutes. Individuals that traveled to the coast of Africa averaged 11.5 ± 7.8 dives per sample period, while those migrating northwards into the Aegean Sea averaged slightly fewer, at 10.3 ± 6.1 dives per sample period. Turtles migrating southwards also took slightly shorter dives on average (mean ± SD = 18.2 ± 16.9 minutes) than those migrating to the north (24.2 ± 21.2 minutes) and spent less time at the surface (Africa: 54.5% of dive time and Aegean: 71.8% of dive time).

During SSSM-designated area-restricted search (behavior mode 2), turtles (n = 15) averaged (± SD) 10.6 ± 9.6 dives per sample period, 18.6 ± 20.0 minute dives and spent 30.4% of dive time above 5 m of depth. There were slight differences in the dive behavior during SSSM behavior mode 2 for turtles from the 3 different regions. Individuals that maintained residency in the Aegean Sea performed the most dives on average (Aegean: mean ± SD = 12.3 ± 9.5 dives; African: 9.88 ± 11.3 dives; Cretan: 8.27 ± 5.9 dives), with
the slightly shortest mean dive duration (Aegean: 17.3 ± 18.9 minutes; African: 17.4 ± 20.3 minutes; Cretan: 24.5 ± 21.5 minutes) and there was a significant difference in the amount of dive time spent closest to the surface (Aegean: 37.1%; African: 25.3%; Cretan: 25.2%; p < 0.001, F2, 736 = 14.7). These regional differences, however, are most likely due to the duration of available data, as the transmitters on the Cretan turtles lasted the longest. Thus, the data for Cretan turtles included a higher amount of overwintering behavior (i.e., fewest dives per sample period, longest dive durations and shortest amount of time spent at the surface), compared to the other regions.

**CPA analysis**

Using changepoint analysis on the complete data set of rates and directions of movement of the postnesting turtles, along with seven measures of dive depths and diving activity patterns, we were able to distinguish three separate and distinct modes of behavior along with transition phases between each major behavioral shift (Table 1; Figs. 3a, b and 4). We classified the five identifiable behaviors as the three behavioral modes migration, foraging, and overwintering and two transitional phases between these modes.

For the 15 turtles that traveled away from Crete, the first behavioral mode (CPA1) after completion of the nesting season was categorized as migration. Although this behavioral mode may have included some days of resident foraging for the turtles that migrated northwards, turtles in this mode averaged rates of travel 23.0 km per day (±8.9), only slightly less than the SSSM transiting mode. In further comparisons, there were more dives (14.1 ± 8.7 dives per sample period), shorter dive durations (16.0 ± 14.9 minutes), and slightly less dive time spent above 5 m of depth (52.3%) in the CPA migration mode than the SSSM transiting mode.

Similar to the SSSM analysis, there was a significant difference in the number of dives per sample period between regions, with the north-
ern migrating turtles averaging the most dives (Aegean: mean ± SD: 15.4 ± 8.7 dives; African: 10.9 ± 7.8 dives; p < 0.0001; F1,288 = 17.4), shorter dive durations, and slightly less time closer to the surface (Aegean: 14.7 ± 13.1 minutes; 51.5% of dive time; African: 20.0 ± 18.9 minutes; 53.8% of dive time).

Behavior mode T1-2, as calculated by the CPA, represented the first observed transition phase, which occurred between migration (or nesting) and foraging. Such a transition phase was observed for 14 turtles, while 3 individuals exhibited an abrupt change to apparent foraging and far more localized movement. For several turtles this transition behavior included a slowing of travel to a mean rate of 11.0 ± 5.8 km per day, but not a change in turn angle. The periods of transition in CPA mode T1-2 ranged from 6 to 39 days (20.8 ± 10.8), with turtles that traveled northwards exhibiting the shortest transition periods, and those remaining near Cretan waters exhibiting the longest.

The CPA-identified transition mode T1-2 also was characterized by a decrease in mean dives per sample period (mean ± SD = 12.5 ± 8.9) and a slight increase in mean dive duration (16.6 ± 15.6 minutes), along with a significant decline in the amount of time spent above 5 meters (43.4% of dive time; p = 0.01, F1,416 = 6.11).

Behavioral mode 2 (CPA2), as calculated by CPA, was categorized as foraging. For the turtles that we were able to track into overwintering (n = 8), foraging lasted an average of 70.3 ± 33.0 days; for the remaining turtles (n = 9), foraging apparently continued for the remainder of the duration of transmissions. Foraging, CPA2, was characterized by a greatly diminished and proscribed rate of travel (10.7 ± 2.7 km per day), a slight decrease in mean rate of diving (11.2 ± 9.83 dives/period), an increase in mean dive duration (19.1 ± 18.5 minutes) and a significant decline in the amount of time spent above 5 m of depth when compared with migration and the transiting 1-2 behaviors (32.0%; p < 0.0001; F2,749 = 32.0). During the CPA foraging mode there was a significant difference regionally in the number of dives per sample period (p = 0.01, F2,415 = 4.50), with turtles migrating to Africa averaging the highest number of dives (African: 12.5 ± 11.3 dives; Aegean: 10.2 ± 8.4 dives; Cretan: 9.12 ± 6.0 dives) and taking shorter dives (African 16.0 ± 15.3 minutes; Aegean: 22.8 ± 23.1 minutes; Cretan: 22.7 ± 17.8 minutes) than those remaining in more northern waters. Throughout the foraging months for all regions, sea surface temperatures averaged 25.5° ± 2.2°C; southern waters were warmer, averaging 26.2° ± 2.3°C, the Aegean Sea averaged temperatures of 24.5° ± 1.8°C.

Eight turtles were tracked beyond the CPA foraging period, as they moved into an apparent overwintering behavioral mode. Two individuals exhibited a type of transition behavior between foraging and overwintering (T2-3) starting in October, and 6 turtles shifted directly into an overwintering behavior, CPA3. The dates when CPA overwintering began showed no distinct regional trend, and varied considerably between the dates of 13 October and 22 January. Average sea surface temperature during late October was 21.0° ± 1.5°C, with the Gulf of Gabès region being typically 2°C warmer than the Aegean Sea. During the CPA overwintering period, mean sea surface temperature in the Gulf of Gabès region was 15.9° ± 2.3°C; near Crete it was 18.5° ± 2.1°C; and in the Aegean Sea was 17.2° ± 1.4°C. The lowest sea surface temperature recorded by the transmitters during CPA overwintering was 13.4°C, recorded in February near the Gulf of Gabès.

The transition phase between foraging and overwintering, T2-3, was characterized by increased standard deviations in both dives per sample period (mean ± SD: 12.7 ± 15.7) and dive duration (16.6 ± 19.7). Additionally, a significant reduction (p < 0.0001, F3,775 = 25.5) in the amount of time spent in the upper 5 m of the water column during this behavior indicated a switch to a more sedentary phase (21.2% of time).

This pattern of reduced time in the upper water column was more extreme during the CPA overwintering phase, with a mean of only 11.0% of dive time spent in the upper 5 m. In addition, mean dive durations increased greatly to 64.1 ± 40.7 minutes, accompanied by a reduction in the mean dives per sample period to only 2.2 ± 2.6. Both parameters were significantly lower than those observed in all previous CPA behavior modes (p < 0.001, F4,906 = 50.8 and p < 0.001, F4,1067 = 44.2, respectively). All combined, the turtles exhibiting this CPA overwintering mode...
appeared to be very inactive and mostly sedentary, presumably resting on the bottom.

**DISCUSSION**

With the addition of multiple sensors, modern transmitters can measure and record much more than two-dimensional location data. The use of changepoint analysis, which combined multiple horizontal and vertical movement parameters, revealed a detailed and comprehensive view of the at-sea behavior of loggerhead turtles in the eastern Mediterranean. Using a Bayesian switching state-space model (SSSM) on Argos satellite location data, we were able to detect shifts in behavioral states between transiting, and what has been termed area restricted search (Jonsen et al. 2007, Bailey et al. 2009). These behavioral states were interpreted in our study as migration and foraging. However, the distinction between behaviors was likely limited by the number of parameters that were incorporated into this SSSM analysis.

In CPA, we were able to easily incorporate additional measurements of dive depths, dive durations, and proportion of time at specific positions in the water column, along with derived parameters such as ranges, variability, and frequency of diving and movement metrics. In effect, the application of CPA on several simultaneous metrics enabled an effective use of the available telemetry data and revealed 5 unique behaviors, with 3 categorized as major behaviors and 2 as transition phases; yielding a more detailed account of at-sea behavior and how behavioral changes can have different movement characteristics. The CPA approach allowed us to identify the number of changepoints based on a suite of movement parameters. A general limitation for both models was the

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**Fig. 4.** Dive behavior during each CPA behavior mode for all turtles. On the x-axis, 1 = “CP 1”, 2 = “T 1-2”, 3 = “CP 2”, 4 = “T 2-3” and 5 = “CP 3”. Sample periods were 4 hours. Horizontal bars = median; box = 50%; whiskers = range of observations within 1.5 times the interquartile range from edge of the box; circles = observations farther than 1.5 times the interquartile range.
overall lifespan of the transmitters, for example, the number of turtles we identified exhibiting the CPA overwintering phase (CPA3) was directly related to the number of transmitters still functioning during the late autumn and winter months. In our study we do not suspect the cessation of transmissions corresponded to turtle mortality, but simply battery exhaustion (Hays et al. 2007) as limiting transmissions per day in 2011 resulted in a substantial increase in the overall lifespan of the transmitters.

Where the results of the two analytical methods overlapped, the largest difference found between SSSM and the CPA was the interpretation of the migration phase. The SSSM calculated that this first behavior lasted an average of 24.3 ± 19.1 days, whereas behavior mode CPA1 was calculated to be 36.2 ± 12.9 days. Most of the discrepancy could be attributed to several turtles that traveled northwards into the Aegean Sea for which the behavior CPA1 duration was calculated to be, on average, 40 days longer than the comparable SSSM migration behavioral mode. Thus, although the Aegean turtles had reached the general area in which they ultimately established residency, their dive behavior, according to the CPA was still characteristic of migration for several more days, meaning a high number of short shallow dives. As a result, despite the wide range in migration distances, which differed by as much as 2300 km, the amount of days it took for the Aegean and African turtles to migrate and complete the transition phase was not significantly different (p = 0.1, F1,11 = 2.9), nor were the starting dates of foraging between destination sites (CPA2 start date: p = 0.4; F1,11 = 0.670). However, the turtles that remained in the waters around Crete began foraging significantly quicker after nesting (p = 0.02, F2,13 = 5.3) and there was a significant difference in starting dates (CPA2 start date: p = 0.002, F2,13 = 9.89). Thus, without the necessity of migrating, foraging could begin much sooner for those four turtles that stayed in waters nearby to the nesting site.

Loggerhead turtles foraging in North African waters of the Mediterranean exhibited the highest number of dives per sample period per foraging area, suggesting they had the highest activity levels. Increased diving activity may correspond to higher water temperatures, which averaged 2°C warmer in North African waters than in Aegean. We observed that turtles remaining in Aegean and Cretan waters, where water temperatures were similarly lower, displayed similar levels of diving activity while the African turtles were far more active during foraging. Similar results were reported by Godley et al. (2003), where two loggerheads tracked by satellite from Cyprus exhibited longer submergence times during foraging than individuals in waters approximately 2°C warmer. Increased diving activity may reflect higher basal metabolism due to increased temperatures, or could reflect more searching in less food-rich waters (Patel et al. 2015).

As our analytical capabilities improve with techniques such as SSSM and CPA, we can distinguish much more subtle differences in behavior from remotely sensed data. By determining shifts in at-sea behavior, we can examine correlated patterns of important environmental factors and estimate and predict interactions with fisheries and other potentially disruptive human activities. Finer resolution of when and where sea turtles and other marine animals migrate, feed and reproduce can be used immediately to develop effective conservation plans and to implement best management decisions that regulate spatial and temporal use of specific regions and habitats. For example, loggerheads cross the Eastern Mediterranean Sea annually migrating from nesting beaches to feeding areas during August and September. During their migratory behavior, these turtles take several short dives, spending more than 50% of dive time in waters shallower than five meters. As a result, regulating longline and net fisheries during these months in terms of specific locations, placement and depth of set of hooks and nets could greatly reduce undesired bycatch. Similarly, by determining specifically when and where overwintering behavior begins and ends, bottom trawling could be limited in certain areas during those months.

Two of the postnesting migration patterns observed here have been reported for loggerheads from other nesting beaches in the Mediterranean. Postnesting females from Zakynthos, Greece and from Cyprus were tracked to North Africa, including several individuals that settled in Tunisian shelf waters (Margaritoulis et al. 2015).
2003, Broderick et al. 2007, Zbinden et al. 2008, 2011, Schofield et al. 2013). In addition several loggerheads from Zakynthos were tracked as they migrated to Aegean waters (Schofield et al. 2013). Notably, the third postnesting pattern, in which turtles remained resident in Cretan waters, has not been documented before. However, this was similar to the behavioral pattern of a loggerhead nesting on Cyprus which was observed to migrate only a short distance to remain within Cypriot waters in consecutive postnesting migrations two years apart (Broderick et al. 2007). Additionally, unlike western Greek nesting populations, we did not track turtles migrating into the Adriatic Sea. Flipper tag return data has also shown a general lack of migration from Rethymno into the Adriatic Sea with only 1 tag recovered (Margaritoulis and Rees 2011). This may indicate unique oceanographic conditions impacting the dispersal of turtles from this beach (Hays et al. 2010).

Overall, the majority of turtles tracked in the various telemetry studies in the Eastern Mediterranean Sea traveled through the Exclusive Economic Zones of seven countries, Cyprus, Egypt, Greece, Italy, Libya, Tunisia and Turkey. These countries are responsible for 63.7% of the captures of sea turtles by fishing gear annually in the Mediterranean (Casale 2011). For the best solutions to such pressing problems, we need to make the most effective use of our remote telemetry data using advanced analytical techniques, such as presented here. For both fisheries management and conservation of biodiversity, it is crucial, and indeed an achievable goal, to find an acceptable balance among limited bycatch, sustainable harvest, and economic gain (Howell et al. 2015).

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