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Normalizing home ranges of immature Kemp's ridley turtles (*Lepidochelys kempii*) in an important estuarine foraging area to better assess their spatial distribution

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ABSTRACT

Kemp's ridley turtles (*Lepidochelys kempii*) are critically endangered sea turtles that forage seasonally in Chesapeake Bay, a large estuary on the east coast of the United States. Most of the Kemp's ridley turtles foraging in the bay are immature. When tracking these animals, satellite transmitter retention times have been low compared with adult marine turtles of other species. The immature Kemp's ridleys' small size and rapid growth leads to shorter, more variable deployments, limiting the use of data. These limited data leave critical questions remaining about the animals' habitat usage that are difficult to answer without substantially more deployments. A novel sensitivity analysis using simulated deployments indicated that too few animals were tagged with satellite transmitters to identify all possible home-range areas in the Bay. We used simulation to create animal deployments of equal duration to address biases (differing lengths of deployments and time between locations) in home-range analyses and boost the information available from relatively short deployments. Combined home ranges from simulated deployments identified important areas for these animals in the south-western portions of the Chesapeake Bay and in the nearshore areas of the Bay north to the middle of the Bay. These areas represent opportunities for managers to mitigate impacts from boating, dredging, military activities and fishing, and could inform critical habitat designations under the United States Endangered Species Act. Habitat modelling may be needed to identify additional important areas in the Bay where animals were not observed via satellite tracking.

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Introduction

The Kemp's ridley turtle, *Lepidochelys kempii* (Garman, 1880), is one of seven extant species of marine turtle, and its distribution is generally limited to the Gulf of Mexico and the continental shelf of the north-western Atlantic Ocean (Pritchard and Marquez 1973; Marquez 1994; Wibbels and Bevan 2019). This species is listed as endangered under the United States Endangered Species Act (List of Endangered Foreign Fish and Wildlife 1970; United States 1983) and subsequent amendments, and as critically endangered by the International Union for the Conservation of Nature (Wibbels and Bevan 2019). As such, there is a critical need for information regarding distribution patterns of this species to facilitate conservation efforts.

It is well documented that Virginia coastal and estuarine waters, including Chesapeake Bay (the Bay), are seasonal, developmental foraging habitats for immature loggerhead [*Caretta caretta* (Linnaeus, 1758)] and Kemp's ridley turtles (Lutcavage and Musick 1985; Keinath et al. 1987; Seney and Musick 2005; Mansfield 2006; Mansfield et al. 2009). The Bay is a large, temperate estuarine complex on the east coast of the United States, and annual changes in ambient water temperature limit cheloniid sea turtle residency times from May until early November (Mansfield et al. 2009).

Sea turtles migrate into the Bay in late spring when water temperatures reach ~20°C (Mansfield et al. 2009) and migrate south in the autumn as temperatures drop, although some cold-stunned individuals strand each year (Barco et al. 2015). Adult Kemp's ridley turtles are less common in Chesapeake Bay but have been observed during several nesting events since 2012 (T. Boettcher, personal communication, 2 June 2020). Individual immature Kemp's ridley turtles have been shown to return to the same seasonal foraging areas, such as Chesapeake Bay, in subsequent years, despite the difficulty in recapturing individuals in-

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water between foraging seasons (Lutcavage and Musick 1985; Mansfield 2006). Additionally, some sea turtles exhibit fidelity to areas with high prey abundance (Broderick et al. 2007; Shaver and Rubio 2008; Marcovaldi et al. 2010). Kemp's ridley turtles in Chesapeake Bay feed primarily on blue crabs (*Callinectes sapidus* Rathbun, 1896), which are prevalent in the region in shallow, estuarine areas within the Bay (Byles 1988; Seney and Musick 2005; Barco et al. 2015).

In the Bay and the nearshore environment around its mouth, Kemp's ridley turtles face various threats, including, but not limited to, nearshore vessel traffic into and out of the seventh busiest port in the United States (Barco et al. 2015; Panjiva 2019), military traffic from the world's largest naval base, frequent dredging to maintain shipping channels, military exercises, commercial and recreational fishing efforts, and climate change. Of particular concern are the navigable waters used by watercraft. During 2011–2017, the time period of the current study, 349 dead, stranded Kemp's ridley turtles were reported in Virginia, and 112 of those (32%) showed signs of vessel interaction (Swingle et al. 2018; Susan Barco 2019, unpublished data). For 103 of the 112 cases (92%), the interaction was listed as the probable cause of stranding (Susan Barco 2019, unpublished data). Most carcasses were not in good enough condition to make a definitive cause of death determination, which only occurs following sample collection and review by a veterinary pathologist, but vessel interaction was the cause of death in 92.8% of stranded sea turtle cases where signs of vessel trauma were observed in Florida (Foley et al. 2019), making the Virginia numbers consistent with other studies. The next most common cause of stranding was cold stunning with 26 cases (Susan Barco 2019, unpublished data). More than 27% (95 of 349) of the turtles examined had no apparent injuries. For marine mammals (Moore et al. 2013) and sea turtles (Barco et al. 2016), this finding is consistent with underwater entrapment in fishing gear.

The varied threats to Kemp's ridley sea turtles in Chesapeake Bay, and the Bay's importance as a summer foraging area, require detailed knowledge of the distribution patterns for this species to inform conservation efforts and potential critical habitat designations under the ESA. Any identified high-use areas need to be supported by robust data and analytical methods given the complex overlap of marine turtle and human uses of the Bay. The identification of animal home ranges for the Kemp's ridley turtles in the Bay will provide managers with the spatial information needed to inform conservation efforts.

The home range of an animal can be defined as the area traversed by the animal during its normal activities (Burt 1943). The utilization distribution (UD) (Van Winkle 1975) was developed to quantify the original definition of home ranges and was used in the current study. The UD can be described as a density function that assesses the probability that an animal will relocate at any place according to the coordinates (x, y) of the place (Silverman 1986).

The results of a home-range analysis can only reflect the animal location data used to generate it. Argos satellite (http://www.argos-system.org) transmitters are commonly used to locate telemetered animals via a transmitted radio signal triangulated by a suite of satellites. This technology, although powerful, has limitations, such as location error and irregular time intervals between locations, that affect the usefulness of the home ranges derived from these locations (Hays et al. 2001).

It can be financially and logistically prohibitive to acquire adequate sample sizes for the resulting home ranges to be representative of the population in a study area as large as Chesapeake Bay. When comparing individual home ranges, many factors can affect observed differences among animals, including length of deployment (because of animal death, transmitter loss, battery life), time of year, location of release, and autocorrelation between locations. Otis and White (1999) stated that autocorrelation between locations can only be ignored in tracking studies if enough locations are sampled over a fixed period of time. An unknown, minimum number of locations is required to generate an accurate home range (Harris et al. 1990) that may not be met with relatively short deployments.

Kemp's ridley turtles can be difficult to tag in Chesapeake Bay and nearshore waters off Virginia. They tend to dive or swim away quickly when approached for in-water capture, and their small size and fast growth rates (Seney et al. 2010) make transmitter attachment and retention challenging. Also, smaller antennae and switches on transmitters suitable for immature Kemp's ridley turtles frequently become fouled or damaged in Chesapeake Bay, with its shallow grass beds and numerous structures covered with barnacles and oysters. One hypothesis for poor satellite transmitter performance on smaller turtles (including immature Kemp's ridleys) is that rapid growth rate combined with rigid epoxy adhesives can be detrimental to retention or normal turtle growth (Seney and Landry 2008). As turtles grow, their scutes expand and a rigid adhesive cannot expand with the scutes. This forces either the scutes to deform to accommodate

the adhesive or the adhesive to lose contact with the carapace.

Animal movements can be simulated by using the R (R Core Team 2019) package *crawl* (version 2.2.1; Johnson and London 2018) to analyse movement parameters from telemetered animals. Although simulated deployments do not fully reflect empirical location data, using movement parameters from a variety of individuals increases realism and allows several improvements to animal home-range studies. Deployment durations can be 'evened out' so that animals have equal contributions to home-range analyses, and simulated deployments can be used to 'boost' the number of deployments in an analysis when deploying additional transmitters in the field is infeasible. Sensitivity analyses can be undertaken to determine the number of deployments before all occupied areas could be empirically identified, assuming simulated animals move like real animals.

In the current study, we used immature Kemp's ridley turtles equipped with Argos satellite transmitters released in southern Chesapeake Bay and simulation to examine animal home ranges primarily within Chesapeake Bay. We also perform a sensitivity analysis to determine how many animals would need to be deployed to empirically identify all available use areas within the study area.

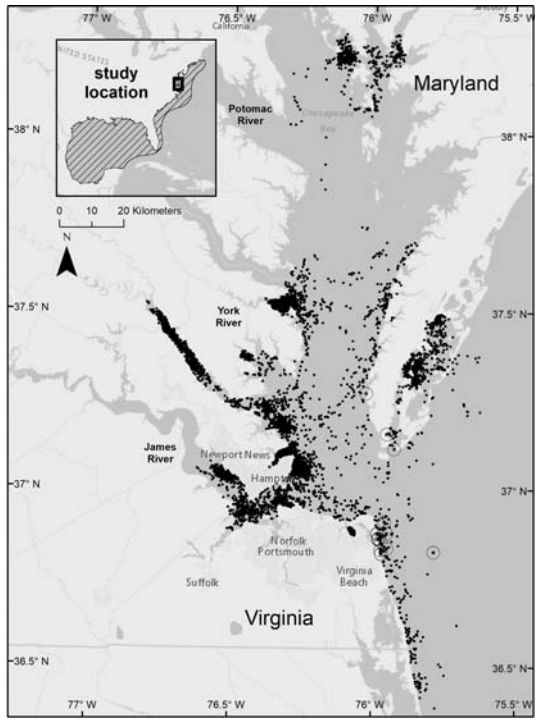

Figure 1. Filtered Argos satellite locations (black dots) and deployments locations (circled stars) for 20 Kemp's ridleys (*Lepidochelys kempii*) deployed in or near Chesapeake Bay. The inset map shows the study location on the east coast of the United States and the range of the species (hashed polygon).

Methods

Satellite transmitter attachment

Kemp's ridley turtles (*Lepidochelys kempii*) were deployed with satellite transmitters in 2011 and from 2013 to 2017 during the summer foraging seasons. Efforts were made to deploy transmitters early in the season, typically May or June, to maximize the time animals spent telemetered in Chesapeake Bay (Figure 1).

Turtles were acquired using two methods: (1) direct capture by researchers using a dip net ($n = 1$) or (2) rehabilitated animals that were either stranded ($n = 7$) or captured on hook-and-line by recreational anglers ($n = 18$). In general, animals were rehabilitated for less than two weeks before release.

All rehabilitated turtles underwent a full health assessment at the Virginia Aquarium & Marine Science Center located in Virginia Beach, Virginia, USA, and were cleared by veterinary staff prior to release. Blood was drawn to perform a basic health assessment in addition to a physical examination. Wild-caught animals with a heavy epibiont load or that were visibly malnourished, injured or missing an appendage did not receive transmitters.

Turtles that cleared the health assessment received satellite transmitters, Inconel flipper tags, and passive integrated transponder (PIT) tags. Inconel tags are small metal tags (~3 cm in length) that are clipped to the trailing edge of both rear flippers and are stamped with a serial number. These indicate to other researchers that this animal has been previously captured and studied. The PIT tag, about the size of a grain of rice, is inserted into the triceps muscle of one of the front flippers using a large bore needle. The PIT tag is unpowered but transmits a serial number when passed over by a receiver. It serves the same purpose as the Inconel tag but is not visible outside the animal and is usually a longer-term passive tag than Inconel tags.

Several models of Argos satellite transmitters were used and, for rehabilitated turtles, per United States Fish and Wildlife Service permit requirements (USFWS 2016), only transmitters that would produce less than 10% drag on an animal and weighed less than 5% body weight, including epoxy, were attached. Drag was calculated using graphs and tables from Jones et al. (2011).

Prior to Argos transmitter attachment, the carapace of each turtle was prepared by removing epibiota and dead scute tissue with putty knives and coarse (60–100

grit) sandpaper. After sanding, the scutes were wiped clean and washed with acetone. Sika Anchorfix-1™ epoxy was used for transmitter attachments on all turtles. The epoxy was used to create a teardrop-shaped footprint on the carapace to improve transmitter hydrodynamics (Jones et al. 2011).

Argos transmitter models included Wildlife Computers SPOT 5 ($n = 2$), SPOT 6 387C ($n = 4$), SPOT 6 311B ($n = 6$), SPLASH 284A ($n = 1$), SPLASH 100 ($n = 3$), SPLASH 309A ($n = 5$); and Sirtrack KG 273 ($n = 2$) and KG 172 ($n = 3$). Multiple models and brands of transmitters were used because of variation in available funds among years and the need to have a range of sizes available for differently sized animals to meet drag requirements while maximizing deployment time through longer battery life. Some transmitters had different expected battery capacities and transmission power, but we have no reason to believe there were substantive performance differences among them for transmitting Argos location data over short time periods. All satellite transmitters were programmed to collect continuous location data because of the anticipated short retention times.

Transmitter attachment for two turtles less than 40 cm straight carapace length notch-to-tip, which was measured as straight line carapace length by placing callipers from the cranial notch at the midline of the carapace to the longest caudal tip of the carapace (Stokes and Epperly 2008), included a layer of flexible neoprene between the carapace and the rigid-epoxy transmitter site (Seney et al. 2010). The neoprene was affixed to the centres of the scutes using rigid epoxy, but the seams between the scutes, where growth occurs, were protected by silicone gasket material, allowing for the silicone and neoprene to stretch as the animal grows. Table I summarizes data for all deployments retained in the analysis, including transmitter make and model, release date and location, turtle length, total body mass collected using spring or platform scales (depending on the size of the turtle and what was available at the time of weighing), and number of days transmitted.

Satellite data preparation

Six deployed transmitters either did not transmit or had too few transmissions for analysis and were excluded, further limiting the number of telemetered animals available for the current study. Returned Argos satellite locations for the remaining 20 turtles (Figure 1), which are locations derived from Doppler effect measurement of radio transmissions from the transmitters, were run through the Douglas filter (Douglas et al. 2012) to remove unrealistic Argos locations using settings recommended for hardshell turtles by the Turtle Expert Working Group (2009). Argos location errors can be up to five kilometres or greater depending on the quality of the satellite fix (Boyd and Brightsmith 2013). Thus, Argos locations are not true animal locations. The Turtle Expert Working Group Douglas filter settings included parameters for the Maximum Redundant Distance filter and the Distance Angle Rate hybrid filter algorithm that were used to account for unrealistic animal speeds and turning angles. All Argos location classes except for 'Z' were retained unless identified as outliers by the Douglas filter (e.g. travel to the location would have resulted in unrealistic animal speeds or turning angles), as even less accurate Argos locations can inform movement models. Turtle locations received during the first 24 h of transmission also were removed from the analysis to account for possible behavioural changes associated with captivity and handling.

Filtered locational data were manually assessed to remove any additional erroneous locations. For example, two turtles were traversing the seaward side of a barrier island and appeared to cross the landmass but there were no inlets to permit such movements. Several offshore locations were removed for one turtle that was clearly resident in an inlet. The offshore locations would have meant the animal was rapidly moving between the inlet and several kilometres offshore multiple times per day in less than two-hour intervals. All retained Argos deployments had at least 100 locations remaining after automatic and manual filtering was applied (Table I).

Deployment simulation and home range

Movement parameters (velocity, velocity autocorrelation and animal activity) were estimated for each deployment using the R package *crawl*. Initial parameters were set based on recommendations for seal models (Johnson et al. 2008; Johnson and London 2018). Movement models initially developed for marine mammals have previously been shown to be applicable to sea turtles (Jonsen et al. 2007; Maxwell et al. 2011; Hart et al. 2012). The model takes Argos location error into account when estimating locations and estimates locations at equal time intervals, addressing two shortcomings of working with Argos location data. Model diagnostics were examined to ensure goodness of fit prior to simulating deployments. These movement models were then used to generate simulated deployments from each animal.

Table I. Summary of Kemp's ridley turtles released in Chesapeake Bay 2011–2017.

PTT	Tag Manufacturer	Tag Model	Release Date	Latitude (°N)	Longitude (°W)	SCL n-t (cm)	Mass (kg)	Days Transmitted (#)	Filtered Argos Locations (#)
108054	Wildlife Computers	SPLASH-100	29-Jun-11	36.876	−75.948	36.9	6.5	16	652
129021	Wildlife Computers	SPLASH-284A	21-Jun-13	36.833	−75.947	44.0	14.0	20	1392
132367	Wildlife Computers	SPOT-5	9-Jul-14	36.909	−75.956	36.0	7.0	34	350
138114	Wildlife Computers	SPLASH-10 309A	20-Oct-14	37.156	−75.950	42.4	12.8	128	2462
138117	Wildlife Computers	SPOT-5	2-Sep-14	36.859	−75.977	35.4	6.5	36	383
148886	Wildlife Computers	SPLASH-10 309A	29-May-15	36.824	−75.783	50.5	18.0	43	486
148889	Wildlife Computers	SPLASH-10 309A	16-May-15	37.271	−76.023	45.0	16.4	57	1038
150767*	Wildlife Computers	SPOT-278C	5-Jul-15	36.862	−75.976	35.4	6.2	9	317
159707	Wildlife Computers	SPOT 6-287C	19-May-17	36.819	−75.967	39.3	8.1	60	990
159708	Wildlife Computers	SPLASH-10 309A	2-Jul-16	36.829	−75.969	45.2	11.9	33	304
159709	Wildlife Computers	SPLASH-10 309A	26-Jul-16	36.855	−75.967	49.4	16.3	31	302
161472*	Sirtrack	K2G 273	22-Jul-16	36.862	−75.976	34.2	5.6	39	652
169763	Sirtrack	K2G 172	8-Jun-17	36.875	−75.981	29.2	3.2	29	577
169764	Sirtrack	K2G 172	17-Jun-17	36.875	−75.981	32.1	4.4	36	541
169765	Sirtrack	K2G 172	19-May-17	36.818	−75.967	40.0	8.1	119	1445
169767	Wildlife Computers	SPLASH-10 309A	5-May-17	36.875	−75.981	44.1	11.9	57	307
169768	Wildlife Computers	SPLASH-10 309A	19-May-17	37.11390	−75.92352	45.7	12.0	44	785
169770	Wildlife Computers	SPOT 6-311B	10-Jul-17	36.86019	−75.97659	28.9	3.4	35	653
169771	Wildlife Computers	SPOT 6-311B	30-May-17	36.87530	−75.98090	30.1	3.2	20	275
169772	Wildlife Computers	SPOT 6-311B	10-Aug-17	36.87520	−75.98080	29.8	3.1	10	135

Platform terminal transmitters (PTTs) marked with an asterisk were attached with the neoprene method. Straight carapace length notch-to-tip (SCL n-t) was used to determine turtle length.

A 28-day period, with a 6-hour time interval, was selected as the deployment simulation length. The 28-day period was chosen after experimenting with different simulation lengths. This length represented a compromise between having enough locations to generate UDs within Chesapeake Bay but not extrapolating so much that simulated deployments diverged grossly from reasonable expectations for actual animal locations. The mean length for deployments carried forward in the analysis was 43 days (min = 9, max = 128, SD = 30.2). Six hours was the longest mean time interval between locations for an individual deployment.

For deployments longer than 28 days ($n = 15$), 10 sets of locations were simulated that generally followed the original deployment, essentially truncating the deployment to 28 days. Although some information was lost in the truncation of deployments, having similar length deployments allowed for better comparison spatially, temporally and among individual turtles. For deployments shorter than 28 days ($n = 5$), 10 simulated deployments were created, each a different realization of the movement a turtle could have taken after the actual deployment ended.

Simulated deployments were limited to be in-water by using the Global Self-consistent Hierarchal High-resolution Shoreline (Wessel and Smith 1996, 2017) full resolution dataset as a land boundary. Simulated deployments were compared visually to actual deployments to assess whether simulated deployments appeared realistic, and a minimum convex polygon was created around the Argos locations to see if simulated locations fell within the 'footprint' of the Argos deployments.

Gridded UDs after Maxwell et al. (2011) were generated for each simulated deployment. Ten-kilometre grid cells were selected as a balance between capturing variation within the Bay while encompassing enough locations within each grid cell to generate meaningful UDs. Gridded UDs were selected for ease of interpretation in the sensitivity analysis (see below) and to provide a common surface to combine individual UDs into a joint home-range analysis. The core area of a home range, commonly defined as the

50% isopleth of the UD (Powell 2000), was selected to represent high-use areas for individual turtles. The 90% isopleths were used to represent full home ranges, eliminating outlier locations.

For the joint home-range analysis, each of the 10 simulated deployments for an individual was weighted 1/10 and all locations were used to generate a UD for that simulated deployment. Two combined UDs of simulated deployments were created by combining the 50% and then the 90% isopleths of all individual simulated deployment UDs, counting the number of times a grid cell was selected as falling within one of those isopleths for all simulated deployment UDs. For example, if a grid cell was included in the 50% UD of two different individuals, it would have a value of 2 in the 50% combined UD. The resulting simulated combined UD showed combined occupied areas for the simulated population of turtles, with each animal contributing equally. The number of grid cells in the 90% and 50% isopleths were counted for the individual and combined simulated UDs to summarize area use. This process was then repeated for the non-simulated, filtered Argos locations, creating non-simulated combined UDs to compare with the simulated combined UDs. At no point were Argos locations combined with simulated locations. High-use areas for the combined UDs were defined as grid cells with UD counts in the top two quintiles of the combined UD analyses.

Sensitivity analysis

To examine changes that occurred as deployments were added to the cumulative home-range analysis, a sensitivity analysis was performed. This was done to explore the change in the simulated combined UDs (e.g. use areas) as a proxy for the addition of more deployments. This type of sensitivity analysis is commonly performed with non-simulated deployments (Hawkes et al. 2007; Soanes et al. 2013; Maxwell et al. 2016) but would not have been informative here given the low number of deployments. Each generated realization of a possible deployment (n = 200) was used to generate a UD. No weighting was used when creating the simulated UDs for the sensitivity analysis.

A combined, simulated UD, as described above, was calculated and summary statistics generated for different numbers of simulated deployments, 1–200 individual UDs. Summary statistics were calculated based on the number of grid cells, a proxy for area, in the combined, simulated UDs. Statistics calculated for the combined, simulated UDs included total area (count of grid cells), the number of cells identified by a single deployment, and the proportion of cells identified by a single deployment. This analysis was run 100 times, with deployments being selected at random (with replacement) each time the analysis was run. Deployments were selected with replacement as newly deployed animals could behave very similarly to, or use the same areas as, previously deployed animals. Each simulated deployment acted as a possible realization of a true deployment. The summary statistics from each of the 100 runs were averaged and then compared as the number of deployments included in the combined, simulated UDs increased.

Our goal was to determine at what point new grid cells stopped being added to the combined, simulated UDs. This occurred when: (1) the number of new grid cells reached a plateau as new deployments were added, and (2) the proportion of cells identified by the addition of a single deployment approached zero. Approximate cut-off points were determined by visually examining graphs of the relevant statistics (Figure 5). The following assumptions were made for the sensitivity analysis: (1) average deployment length was 28 days; (2) suitable areas beyond collected turtle Argos locations exist in Chesapeake Bay; and (3) the simulated deployments reasonably represented the movements of animals.

Results

After initial filtering, all 20 remaining deployments successfully had movement models fit using the *crawl* package. All deployments were then simulated 10 times resulting in 200 simulated deployments (Figure 2). A qualitative review of truncated deployments longer than 28 days (n = 15) indicated that simulated deployments generally followed the path of the original deployment locations (see Figure 3 for an example).

Locations that were simulated beyond the original deployment time period were also assessed qualitatively. In each of the 10 simulated deployments for each animal (n = 5), the simulated deployment closely followed the original deployment until extrapolation began. Most extrapolated locations (83%) were within the minimum convex polygon of the original Argos location transmissions. Locations that occurred outside the boundary of the minimum convex polygon defined by the Argos locations were within the known distribution of Kemp's ridley turtles in Chesapeake Bay based on stranding and aerial survey data.

Based on the Argos location data, seven animals spent more than one week in rivers or river mouths,

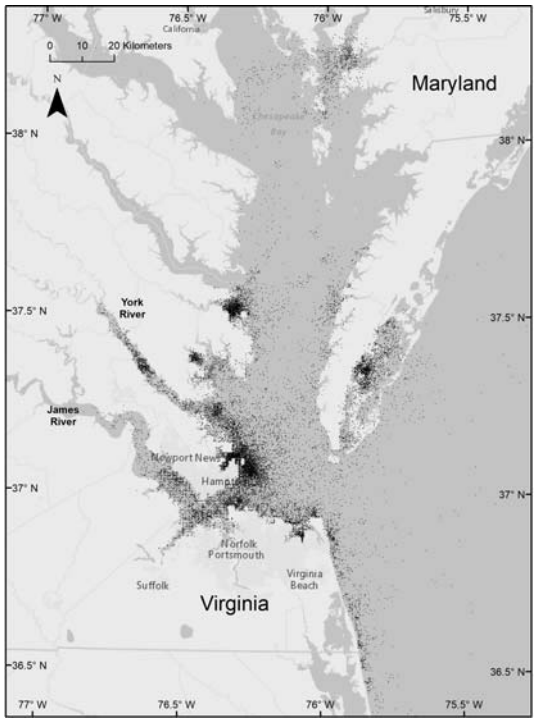

Figure 2. Locations (black dots) from two hundred, 28-day, simulated deployments derived from 20 Kemp's ridley turtles (*Lepidochelys kempii*) equipped with satellite transmitters. The apparent gridded pattern is due to rounding in the output from the *crawl* R package used for the analysis and occurs at a smaller scale than the gridded home-range analysis.

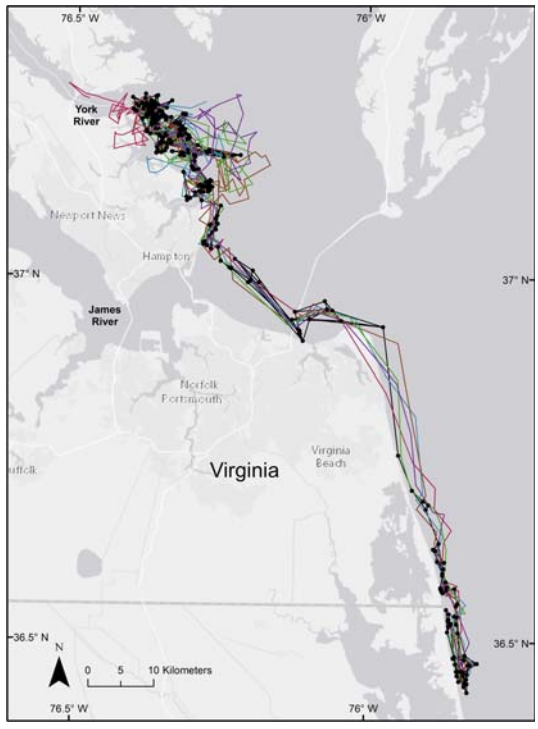

Figure 3. Argos satellite telemetry locations from one deployment (black dots) and path (black line) with five imputed, simulated deployments generated by the R package 'crawl', based on the animal's movement parameters, overlaid (coloured lines).

with two animals spending ~60 days each. Turtles were present as far as 45 km upriver. Two turtles were located primarily outside the Bay during their deployment, just north of the mouth of the Bay. One turtle travelled further north within the Bay, into Maryland waters, and remained there until the end of transmission. The remainder of the turtles were located almost exclusively in the southern areas of the Bay. Three turtles were tracked leaving the Bay in autumn months, presumably beginning their southern migration.

There was no increase in transmitter retention time for the turtles that had transmitters affixed using the neoprene method (Table 1). Both turtles had retention times less than the mean retention time (43 days) for the turtles deployed in the current study.

Home ranges

Areas of all home ranges were measured in the number of 10-km grid cells included in the UD. The mean sizes of home ranges for the 90% isopleths from the simulated deployments were more than five times larger than the 50% isopleths. The number of grid cells in the 90% isopleths ranged from 1 to 38 (mean = 8.9, SD = 6.8). The number of grid cells in the 50% isopleths ranged from 1 to 7 (mean = 1.7, SD = 1.7). Although the spread of individual home-range sizes was similar between the two methods, the mean home-range sizes were smaller for non-simulated, filtered Argos deployments within the Bay, where the number of grids cells in the 90% isopleths ranged from 1 to 36 (mean = 5.6, SD = 7.7) and the number of grid cells in the 50% isopleths ranged from 1 to 10 (mean = 1.1, SD = 2.2). Some of the Argos deployments did not have 50% isopleths as all locations were within a single grid cell. The statistics presented are for only those UDs with a 50% isopleth identified. The means of the 90% isopleths were statistically different between the simulated and Argos deployments (Welch's two-sample t-test, $P = 0.03$) but the means of the 50% isopleths were not (Welch's two-sample *t*-test, $P = 0.1$).

The combined UDs of the filtered Argos locations contained 57 grid cells in the 90% isopleth (Figure 4a) and 15 grid cells in the 50% isopleth (Figure 4b). Note that some grid cells in the figure are covered by the locations. Figure S1 is a version without overlaid Argos or simulated locations. The maximum number of turtle home ranges that

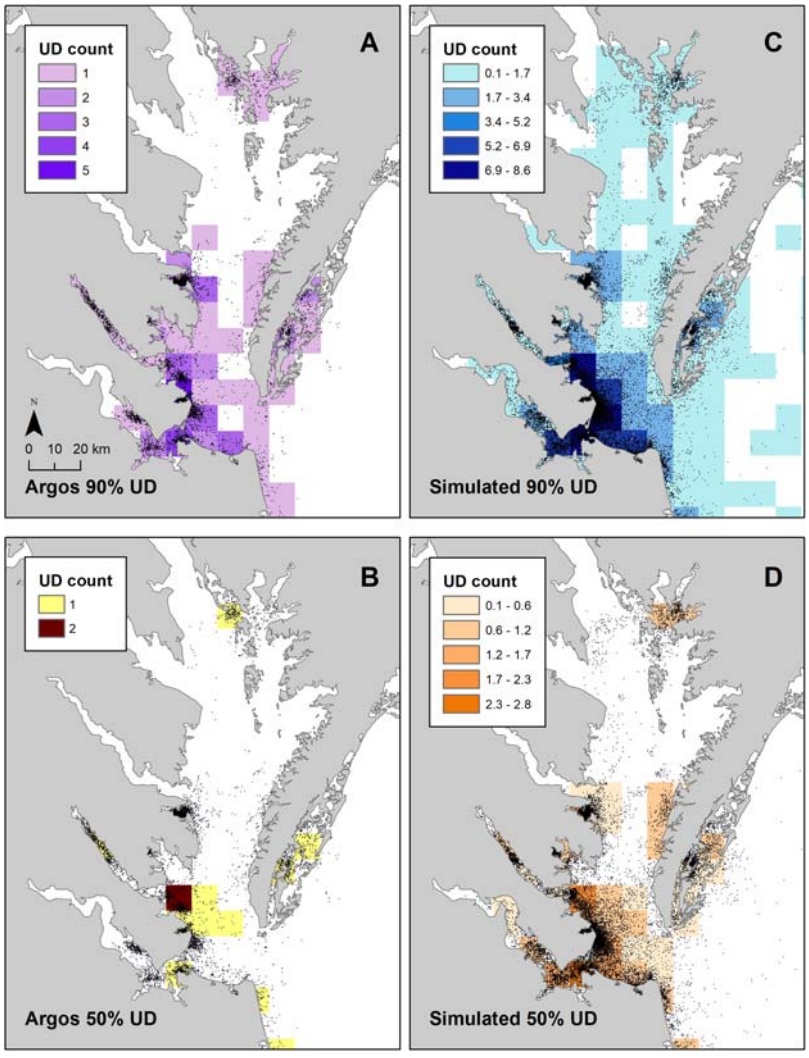

Figure 4. Combined Utilization Distribution (UD) of the 90% (panel A) and 50% (panel B) isopleths for the Argos satellite transmitter locations and combined UD of the 90% (panel C) and 50% (panel D) isopleths of the 28-day simulated deployments. Panels are centred on Chesapeake Bay where most locations occurred. Locations used to generate the UDs are displayed as black dots. Increasing colour intensity indicates increased numbers of UDs that fell within that grid cell. Fractional UD counts are possible in the simulated deployment analyses (panels C and D) as simulated deployments are weighted 1/10. Counts for the simulated UDs were classified into five classes, the top two of which are considered high-use areas.

overlapped with any given grid cell was five for the 90% combined UD and two for the 50% combined UD. The combined UDs of the simulated deployments contained 175 grid cells in the 90% isopleths (Figure 4c) and 47 grid cells in the 50% isopleths (Figure 4d). The maximum number of simulated deployment home ranges that overlapped with any given grid cell was 8.6 for the 90% combined UD and 2.8 for the 50% combined UD. The weighting scheme applied to simulated deployments in the combined UD analysis resulted in fractions of simulated deployments being counted in each cell.

The distribution patterns of home ranges were similar between the simulated and Argos combined UDs, however more grid cells were identified by the simulated combined UD (Figure 4). This was despite truncating deployments longer than 28 days. Additionally, all simulated deployments contributed an equal number of locations to the combined home range, compared with locations from the Argos deployments where there were different deployment lengths and times between locations.

The 90% isopleth from the combined UD for the simulated deployments covered most of southern Chesapeake Bay from the mouth of the Bay to north of the Potomac River, which marks the boundary between the states of Virginia and Maryland. The 50% isopleth of the simulated combined UD showed the core use area of the simulated deployments to be centred near the James and York River mouths of

the south-western Bay with some isolated high-use areas in a topographically complex area to the north. No high-use areas were identified outside of Chesapeake Bay for the simulated deployments (Figure 4). This was true for the Argos combined UD analysis as well.

Sensitivity analysis

As simulated deployments were added to the combined UD analysis, the total area of the simulated combined UD increased and then plateaued (Figure 5a) and the proportion of grid cells identified by the addition of a single deployment approached zero as more simulated deployments were added (Figure 5b). Based on a visual analysis of the proportion of grid cells identified by a single deployment in the sensitivity analysis (Figure 5b), 80–100 deployments would be required to identify most of the possible areas used in Chesapeake Bay where Kemp's ridley turtles have been previously sighted, which generally coincides with the extent of the current study. For this population, assuming 28-day deployments, and movement of new animals being similar to previously deployed animals, new area identified by each additional deployment was less than 2–3% of previous area identified beyond the 80–100 deployment threshold. In the combined, simulated UD, most grid cells began to be covered by multiple deployments, e.g. the area identified approached an asymptote (Girard et al. 2002).

The maximum number of grid cells identified in the combined, simulated UDs (200 individual UDs combined) was 55 for the 90% isopleth and 21 for the 50% isopleth (Figure 5a). In both cases, this was more than the number of grid cells identified in the same analysis using Argos data (Figure 4). The proportions of grid cells identified by a single simulated deployment decreased from 1 to 0.2 for both the 90% isopleth combined UDs and the 50% isopleth (Figure 5b). In each run, variation in the size of the generated UDs occurred as different sets of simulated deployments were selected.

Discussion

Home range

Although Chesapeake Bay is a known seasonal foraging ground for Kemp's ridley sea turtles (Mansfield et al. 2002; Seney and Musick 2005; Mansfield 2006; Barco et al. 2015; Susan Barco 2019, unpublished data), not enough satellite telemetry or in-water sightings research had been performed to define commonly used areas within the Bay itself. In the current study, high-use areas were identified in the south-west corner of Chesapeake Bay, the James and York rivers, and several other nearshore locations in the Bay, although there was extensive variation in home-range size and location among individuals. This variation in home-range size and location was driven by differing behaviour between individuals, as this variation was consistent between the simulated and non-simulated UDs (e.g. home-range variation existed between deployments even when deployment duration was equalized between individuals). As a population, Kemp's ridley turtles may be similar to loggerhead turtles where, as a population, they are generalists in their foraging ranges and behaviour, but individual turtles may specialize in distinct habitats or on specific prey items (Vander Zanden et al. 2010).

The locations of the home ranges generated by our analyses were consistent with prior tracking studies and the known ecology of the Kemp's ridley turtles (Keinath et al. 1987; Byles 1988; Mansfield 2006). These animals generally consume small marine invertebrates, particularly blue crabs (van Engel 1958) and other decapod crustaceans that can be found in nearshore estuarine environments throughout the range of the Kemp's ridley turtle (Millikin and Williams 1984; Van Den Avyle and Fowler 1984). Blue crabs occur seasonally in Chesapeake Bay, particularly near seagrass beds, and have been found in the gut contents of stranded Kemp's ridley turtles (Seney and Musick 2005; Barco et al. 2015). Additional work is needed to determine prey availability and habitat characteristics that may drive these occurrences and to identify other areas not occupied by telemetered turtles.

Kemp's ridleys tracked in the current study were captured in the lower Chesapeake Bay or nearshore ocean waters of Virginia. Historical pound net studies suggested Kemp's ridley turtles also occur in the northern portions of the Bay in the Potomac River (Mansfield et al. 2002) and Maryland Bay waters (Litwiler 2001), though recent evidence for their occurrence in Maryland waters is limited to strandings. It is possible individuals captured in those areas would provide more data on their occurrence in the northern extent of the Bay.

The simulated deployments allowed all animals to contribute equally to the home-range analyses, by equalizing deployment length and irregular time periods between locations that were present in the original deployments. By reducing this variation in tracking data, bias was reduced, though other sources of bias still existed, such as release location. In the context of a home range analysis, location bias

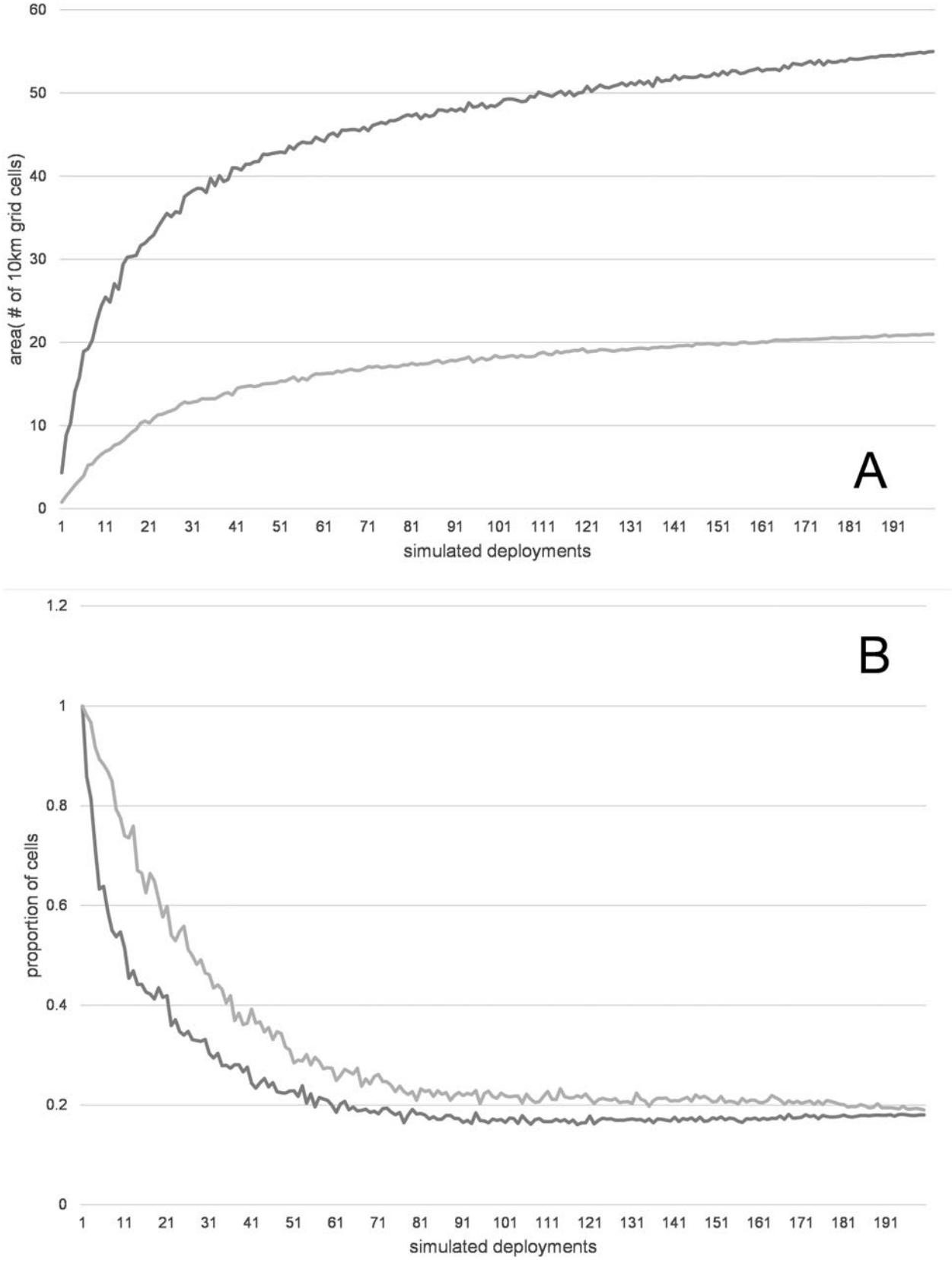

Figure 5. Total utilization distribution (UD) area (number of grid cells, panel A) and proportion of grid cells identified by a single deployment (panel B) as the number of simulated deployments increase. The graphs show that 80–100 deployments would be required to adequately describe habitat use. The light grey line represents the combined 50% isopleths and the dark grey line represents the combined 90% isopleths.

can occur when home ranges are identified close to animal release locations but not elsewhere, even if the animals are known to range more broadly. Differences in the length of time from first to last location can overemphasize longer deployments that have a greater number of locations. Irregular times between locations can bias home ranges toward times when satellite coverage is better or animals are available to transmit.

Our combined, simulated UD analysis did not identify high-use areas outside the Bay owing to the short duration of simulations and the seasonality and location of deployments. Knowing that Kemp's ridley turtles do range outside the Bay shows a limitation to our current study. Simulating longer deployments could have led to identifying high-use areas outside the Bay but we were not confident that longer simulations would have been accurate representations of animal movements. The focus in the current study was movements in the Bay so we aimed to capture turtles as early in the season as possible. Capturing and releasing turtles later in the season may yield better inference into use areas outside the Bay in future studies.

The concurrence of the combined, simulated and non-simulated UDs in identifying high-use areas within the Bay appears to refute that there was an effect from deployment length or irregular time reporting bias in our dataset. This concurrence may be driven in part by all release sites being off the south-eastern coast of the study area. Because the population is migratory, the south-eastern coast is, however, the most likely path that Kemp's ridley turtles travel as they move into the region from the south in spring. We posit that it is more likely that the concurrence is an artefact from the simulated deployments closely following actual deployments, most of which were longer than the 28-day simulation period. Simulating longer than the length of most deployments may have yielded strikingly different areas identified by the simulated versus non-simulated UDs but with lower confidence in the simulated UDs. Even though there was concurrence in high-use areas identified by the two analyses, the simulated combined UD identified more area overall, suggesting that there may be areas in Chesapeake Bay available to animals not identified by the limited number of Argos deployments. We also argue that eliminating potential sources of bias is worthwhile, even if they did not apparently have a large effect on the analysis.

Simulated locations are only as good as the algorithm used to generate them and do not represent true animal locations. As such, results from simulated deployments must be interpreted cautiously. Our analyses were supported by additional sources of data from within the Bay, such as aerial survey sightings, bycatch, and stranding data, that lend credence to our simulated locations. The tradeoffs of increased simulation versus confidence in results must be carefully weighed. Here, considering the limited number of animals available for deployment (relative to the number needed to identify all possible use areas), the short transmitter retention times, and the critical need for management information, we feel the tradeoffs were worthwhile.

Multiple potential hazards to marine turtles occur in Chesapeake Bay, including but not limited to, naval activities from the several nearby military installations, dredging, vessel activity, and commercial and recreational fishing. Bycatch and vessel strikes are common in the region and represent an ongoing source of mortality for this population and for other species of marine turtles in the Bay (Barco et al. 2015; Santos et al. 2018). Determining high-use areas for sea turtles in Chesapeake Bay is critical to determining possible overlaps with stressors and to mitigate impacts. The high-use areas identified in the current study could be used as part of a comprehensive assessment of potential critical habitat under the ESA or to develop mitigation strategies to reduce anthropogenic sources of serious injury and mortality from late spring to early autumn when Kemp's ridley turtles are present and actively foraging.

A surprising result of the home-range analysis was how much time several animals spent upstream of river mouths and how far upstream from the river mouths they travelled, particularly the James and York Rivers (Figure 1). The result was surprising because sea turtles generally do not spend time in brackish or fresh water, although upstream movements have been documented in earlier studies (Byles 1988). More research into the salinity tolerances of these animals is required, but we suspect residency in rivers is driven by the presence of the Kemp's ridley turtles' preferred prey in the area, the blue crab. Submerged aquatic vegetation beds are present in these rivers (Orth and Moore 1984; Orth et al. 1992, 2017), including sea grass beds, and are known habitat for blue crabs. This has implications for management of this species and other marine turtles in the Bay.

Loggerhead turtles, the most abundant marine turtle species in the Bay, frequent deeper areas in the mid-Bay (Barco et al. 2015; Lutcavage and Musick 1985). This contrasts with the apparent distribution of Kemp's ridley turtles in the region, as first noted by Byles (1988). Managing these two species (and

other protected species in the Bay) will require careful consideration to ensure stressors are not shifted to other protected species (e.g. if fishing closures occur in loggerhead turtle habitat and effort shifts to Kemp's ridley turtle habitat). Careful examination of area use by these species is needed to provide additional inference as to whether habitat partitioning is occurring. If more evidence exists that habitat partitioning is occurring between these two species, the challenge of implementing mitigation measures or protected areas that benefit both species is increased.

Two additional species of marine turtles occur regularly in the Bay, leatherback turtles [*Dermochelys coriacea* (Vandelli, 1761)] and green turtles (*Chelonia mydas* Linnaeus, 1758) though in far lower numbers (Lutcavage 1981; Barco and Swingle 2014; Barco et al. 2018). Few green turtles and no leatherback turtles have been tracked in the Bay, making it difficult to determine the extent of overlap with loggerhead and Kemp's ridley turtles. However, if their seasonal presence increases, they may become of equal concern to managers.

Other protected species such as humpback whales [*Megaptera novaeangliae* (Borowski, 1781)], harbour seals (*Phoca vitulina* Linnaeus, 1758), and grey seals [*Halichoerus grypus* (Fabricus, 1791)] occur in the mouth of the Bay seasonally, and bottlenose dolphins [*Tursiops truncates* (Montagu, 1821)] occur year-round (Richlen et al. 2018), further complicating protection efforts. A cohesive strategy to manage all species of concern within the Bay may be possible as more work delineating habitat or home ranges is accomplished for the individual species but will require cooperation from national, state and local agencies, the public, and industry stakeholders. The current study represents a small step toward a more holistic protected species management programme within Chesapeake Bay.

Sensitivity analysis

Our sensitivity analysis indicated that more areas may be available to Kemp's ridleys than utilized during actual deployments and that we had not deployed enough transmitters to identify all possible use areas in the Bay. To deploy another 80–100 transmitters on Kemp's ridleys is infeasible logistically and financially, leaving a gap in our knowledge of this species' habitat use within the Bay. It is unclear if there are even this many Kemp's ridleys available for capture in the Bay as previous aerial surveys did not detect enough Kemp's ridley turtles to derive an abundance estimate (Barco et al. 2018).

Other approaches, such as aerial surveys and habitat modelling, should be used to identify additional possible use areas within the Bay. Aerial surveys can identify use areas without the deployment bias associated with satellite transmitter data but are more expensive and have different types of bias to be mitigated. Habitat modelling has the benefit of linking habitat characteristics to animal presence, helping us to understand possible ecological drivers of animal distribution. However, predictions of habitat outside the known distribution of a species should be undertaken only with caution and interpreted conservatively. The northern extent of Chesapeake Bay, where Kemp's ridley presence is currently considered rare, is such an area. There are numerous examples of linking sea turtle presence, including for Kemp's ridley turtles, to environmental covariates (Abecassis et al. 2013; Putnam et al. 2013; Howell et al. 2015). This presumes that appropriate environmental covariates exist that correlate with animal presence and tie back to sound ecological principles. Chesapeake Bay is a large, complex and dynamic ecosystem and covariates in any habitat modelling approach should reflect that. The availability of these types of covariates are often limited in complex, nearshore environments like Chesapeake Bay. Additionally, in the current study we combined data from multiple years of deployments, and we did not account for inter-annual variability. If animals targeted dynamic habitats, home ranges could shift dramatically among years. In future studies, a habitat modelling approach could account for possible shifts in habitats among years.

We believe the sensitivity analysis approach was valuable as it provided a method to assess whether 'enough' transmitters had been deployed to identify possible use areas without complex statistical methods. This is a common question among resource managers and funders. To our knowledge, this methodology has not been applied before with simulated deployments. It does not require simulation explicitly, though that can complement the process. In past studies, large banks of extant location data have been used to see if new use areas were being identified as deployments were added (e.g. Girard et al. 2002).

Simulation of deployments is most applicable when the area being examined is small or has restricted access, in this case a bay, and when the number of deployments available is relatively high. The amount of location data can be increased via simulation, but this is subject to the caveats and assumptions already discussed above. Although not a solution that can give a firm answer to the question 'how many deployments are enough', it is another tool that researchers and managers can use to inform choices.

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Disclosure statement

No potential conflict of interest was reported by the author (s).

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Data availability statement

The data that support the findings of the current study are available from the Naval Facilities Engineering Command upon reasonable request. Contact Joel Bell or the Marine Resource Specialist Group for permission. They can be viewed on Ocean Biogeographic Information System Spatial Ecological Analysis of Megavertebrate Populations (OBIS-SEAMAP) at http://seamap.env.duke.edu/dataset/1018.

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