1-2018

Consequences of drift and carcass decomposition for estimating sea turtle mortality hotspots

Bianca Santos
Virginia Institute of Marine Science, bsantos@vims.edu

David M. Kaplan
Virginia Institute of Marine Science

Marjorie A.M. Friedrichs
Virginia Institute of Marine Science, marjy@vims.edu

Susan G. Barco
Virginia Aquarium & Marine Science Center

Katherine L. Mansfield
University of Central Florida

See next page for additional authors

Authors
Bianca Santos, David M. Kaplan, Marjorie A.M. Friedrichs, Susan G. Barco, Katherine L. Mansfield, and James P. Manning

Consequences of drift and carcass decomposition for estimating sea turtle mortality hotspots

Bianca S. Santos[1a], David M. Kaplan[1b], Marjorie A.M. Friedrichs[1c], Susan G. Barco[2d], Katherine L. Mansfield[3e], James P. Manning[4f]*

1. Virginia Institute of Marine Science, College of William & Mary, Gloucester Point, VA 23062
2. Virginia Aquarium & Marine Science Center, Virginia Beach, VA 23451
3. University of Central Florida, Biology Department, Orlando, FL 32816
4. National Oceanic Atmospheric Administration, Northeast Fisheries Science Center, Woods Hole, MA 02543

Author email addresses: (a) bsantos@vims.edu; (b) dmk@vims.edu; (c) marjy@vims.edu; (d) sgbarco@virginiaaquarium.com; (e) kate.mansfield@ucf.edu; (f) james.manning@noaa.gov

* **Corresponding author:** bsantos@vims.edu; Phone: 1-804-684-7986

Running title: Drift and decomposition of sea turtles

Abstract word count: 305

Main text word count (from Introduction to end of Discussion): 7832

Figures: 8

Tables: 7

Abstract

Sea turtle strandings provide important mortality information, yet knowledge of turtle carcass at-sea drift and decomposition characteristics are needed to better understand and manage where these mortalities occur. We used empirical sea turtle carcass decomposition and drift experiments in the Chesapeake Bay, Virginia, USA to estimate probable carcass oceanic drift times and quantify the impact of direct wind forcing on carcass drift. Based on the time period during which free-floating turtle carcasses tethered nearshore were buoyant, we determined that oceanic drift duration of turtle carcasses was highly dependent on water temperature and varied from 2-15 days during typical late spring to early fall Bay water conditions. The importance of direct wind forcing for turtle carcass drift was assessed based on track divergence rates from multiple simultaneous deployments of three types of surface drifters: bucket drifters, artificial turtles and turtle carcass drifters. Turtle drift along-wind leeway was found to vary from 1-4% of wind speed, representing an added drift velocity of approximately 0.03-0.1 m/s for typical Bay wind conditions. This is comparable to current speeds in the Bay (0.1-0.2 m/s), suggesting wind is important for carcass drift. Estimated carcass drift parameters were integrated into a Chesapeake Bay oceanographic drift model to predict carcass drift to terrestrial stranding locations. Increased drift duration (e.g., due to low temperatures) increases mean distance between expected mortality events and stranding locations, as well as decreases overall likelihood of retention in the Bay. Probable mortality hotspots for the peak month of strandings (June) were identified off coastal southeastern Virginia and within the lower Bay, including the Bay mouth and lower James River. Overall, results support that sea turtle drift time is quite variable, and varies greatly depending on water and air temperature as well as oceanic

conditions. Knowledge of these parameters will improve our ability to interpret stranding events around the globe.

Key Words

sea turtle strandings; sea turtle mortality; Chesapeake Bay; carcass decomposition; drift leeway; drift simulations; endangered species; conservation

1. Introduction

Coastal strandings of deceased sea turtles provide a unique opportunity to study drivers of mortality in the world's threatened and endangered sea turtle populations (Epperly et al. 1996, Hart et al. 2006). However, interpreting coastal strandings of dead sea turtles can be challenging for a number of reasons. Level of turtle carcass decomposition and/or lack of visible injuries often make determining the cause of mortality impossible. Furthermore, although stranding events provide a general time period and region of mortality, they do not provide a specific space-time location for mortality events that can be directly related to potential causal factors (e.g., human activities, environmental conditions, etc.). Management guidelines have highlighted the need to better understand landfall patterns of stranded sea turtles to infer possible causes of mortality from mortality locations (Turtle Expert Working Group 1998).

Sea turtle carcasses typically sink upon death, until the accumulation of decomposition gases causes the body to bloat and float to the surface (Epperly et al. 1996). At this point, the body is partially submerged and acts as a drifting object. The drift of a deceased sea turtle from death at-sea to a terrestrial stranding location depends on physical forces, namely the direction and intensity of local currents and winds (Epperly et al. 1996, Hart et al. 2006). Forecast models integrating these physical forcing mechanisms can be used to predict the trajectories of drifting objects, including deceased sea turtles. However, the drift characteristics of turtle carcasses, such as the impact of direct wind forcing on carcass movements and the period of time carcasses are positively buoyant and, therefore, capable of significant horizontal movements at the ocean surface, are poorly understood. Careful interpretation of stranding observations based on detailed knowledge of these carcass drift parameters is necessary to better identify probable space-time coordinates of mortality events.

The Chesapeake Bay (Bay) and its surrounding coastal waters are critical forging and developmental habitat for the approximately 5,000 to 20,000 sea turtles (primarily juveniles) who use Bay waters seasonally (Musick and Limpus 1997, Coles 1999, Mansfield et al. 2009). However, a significant number of sea turtle strandings are recorded on local beaches each year. Approximately 100 to 300 sea turtles are found stranded on Virginia's coastline, of which the vast majority are deceased (Mansfield 2006, Swingle et al. 2016). Despite a number of management efforts aimed at reducing turtle mortality, hundreds of turtles continue to wash up every year (National Marine Fisheries Service 2006, Dealteris and Silva 2007, Swingle et al. 2016). Furthermore, as most fatalities potentially go unobserved due to low likelihood of landfall and carcass decomposition, these stranding events may considerably underestimate total at-sea mortality (Murphy and Hopkins-Murphy 1989, Epperly et al. 1996). With all sea turtles within U.S. waters classified as threatened or endangered (National Research Council 1990), there is a pressing need to understand stranding events and identify sources of mortality to ensure population recovery.

Here we address two key uncertainties when estimating mortality locations using stranding data and oceanographic drift simulations: (1) the probable amount of time dead turtles drift before stranding on shore, and (2) the correction to pure oceanic drift needed to account for direct wind forcing on turtle carcasses floating at the surface. A critical factor influencing oceanic drift times is the decomposition rate of carcasses, which controls both how long the carcass will remain buoyant and what decomposition state it will be in when it strands. Carcass decomposition studies are needed to relate the level of decomposition of observed stranded turtles to probable water drift times; however, very limited research on carcass decomposition has been conducted on sea turtles. Higgins et al. (1995) observed the complete decay of two

Kemp's ridleys to occur within 4-12 days; however, one turtle yielded unreliable results due to inconsistencies in sampling protocol between treatments. Furthermore, this study's subtropical location in the Gulf of Mexico may not be representative of the more temperate conditions in our region, the Chesapeake Bay. Intermittent observations noted in Bellmund et al. (1987) of five dead turtles entangled in a pound net in the Chesapeake Bay suggests total decay to occur on a much longer time scale, upwards of 5 weeks, yet detailed information on oceanographic conditions, time of year, or turtle sizes are not presented in the study. The discrepancies in decomposition results, limited ocean temperature range, and small sample sizes highlight the need for controlled field studies relating carcass condition to probable drift time over a range of environmental conditions.

In addition, whereas ocean circulation models are often available to assess the impact of currents, little is known about the impact of direct wind forcing on the surface transport of turtle carcasses. An object's movement through water caused by surface winds is referred to as it's leeway (Allen and Plourde 1999, Breivik et al. 2011). The impact of winds on drifting objects is generally assessed in terms of leeway coefficients representing the fraction of the wind speed that must be added to the along-wind and cross-wind current components to accurately simulate drift patterns (Allen 2005). Field experiments to determine leeway coefficients have been carried out to assess drift characteristics of a variety of objects, such as watercrafts and human bodies, primarily for the purposes of search and rescue operations (Allen and Plourde 1999, Breivik et al. 2011). Some studies have investigated the drift of animal carcasses in relation to likelihood of carcass landfall (Degange et al. 1994), but few provide specific estimates of carcass leeway parameters (Bibby and Lloyd 1977, Bibby 1981). Nero et al. (2013) evaluated turtle carcass leeway from the track of a single tagged moribund turtle, providing the sole estimate of sea turtle wind-induced drift in the literature. There is a noted need to combine experimentally obtained drifter data with oceanographic models to better understand how oceanic conditions affect the flow of carcasses at sea (Hart et al. 2006, Nero et al. 2013, Koch et al. 2013). To address this data gap, we carried out field drift experiments to better estimate the impact of winds on turtle carcass drift patterns (specifically, the along-wind and cross-wind leeway coefficients).

Results from both the decomposition study and the carcass drift experiments were used to parametrize a carcass drift model and provide initial estimates of probable mortality locations from deceased sea turtle strandings data for coastal areas in the Chesapeake Bay. Collectively, the outcomes of this study enhances our ability to infer locations of mortality from stranding events in the Bay, as well as elsewhere around the globe.

2. Materials and Methods

For simplicity in this study, we will use the term "stranding" to refer to the final beached location of a deceased sea turtle. Though stranding datasets often also include data on sick or injured sea turtles that are alive, simulation of the movements of these individuals is greatly complicated by their potential for active swimming, and, therefore, we focus exclusively on deceased individuals.

2.1 Decomposition study

When stranded turtles are found on the beach (which generally occurs within 12 hours of stranding in populated areas), carcass condition is assessed on a condition code scale from 1 (freshly deceased; we are excluding alive code 0 strandings) to 5 (bones) as per the National Oceanographic and Atmospheric Administration's Sea Turtle Stranding Salvage Network (STSSN) stranding report forms and guidelines (http://www.sefsc.noaa.gov/species/turtles/strandings.htm) (Table 1). We conducted carcass decomposition experiments to relate condition codes to probable post-mortem in-water times for a variety of environmental conditions. The decomposition rate of eight juvenile sea turtles, including two loggerheads (*Caretta caretta*), two Kemp's ridleys (*Lepidochelys kempii*) and four greens (*Chelonia mydas*), ranging in size from 26.3 to 68.0 cm straight carapace length notch to tip and 2.38 to 36.5 kg in mass, were assessed during the summers of 2015 and 2016. Carcasses were supplied by the Virginia Aquarium & Marine Science Center Stranding Response Program (VAQS) and Maryland's Department of Natural Resources Marine Mammal and Sea Turtle Stranding Program. Death was attributed to cold-stunning in all cases but one, where lacerations on the carapace of a Kemp's ridley suggested death by vessel strike. All carcasses were assessed with an initial condition code of 1 or 2. Carcasses were frozen prior to use and thawed in a fresh water bath before placement at the study site. Preliminary morphometric measurements were recorded using standard measurement protocols (Wyneken 2001).

A moored buoy system was constructed that allowed for free movement of the carcass throughout the water column and tethered in an area of 3 to 6 ft of water varying with tide in the York River, VA (Figure 1A). A 4-ft helix mooring anchor was installed into the bottom sediment and attached to a bullet buoy with rope. The turtle carcass was wrapped in 4-inch heavy duty polyethylene plastic mesh held together by carabiners and attached to the mooring system using a rope and carabiner (Figure 2). This allowed the carcass to freely move through the water column as its buoyancy changed due to decomposition processes over time. For two trials, a GoPro HERO3+ camera was attached to PVC-pipe embedded in the plastic mesh, and 3-hours of 5-second time lapse photos were recorded daily. The GoPro and PVC-pipe apparatus were adjusted to achieve neutral buoyancy so as not to impede the carcass from floating and sinking.

Approximately every 24-hours during low tide, the turtle carcass was detached from the anchor line and brought to shore where it was thoroughly photographed and qualitatively analyzed, including a detailed description of the carcass decomposition state, its associated condition code and whether it was at the surface or bottom of the water column at the time (Figure A1). As many of the codes are quite broad and can include a wide range of characteristics, early and late categories for each condition code criteria were also recorded. Code 4 is characterized as “dried carcass” by STSSN guidelines, but the turtle carcasses in this study were submerged for the entire trial and did not exhibit this type of desiccation, thus, code 4 was not observed. Temperature data were obtained from the Virginia Estuarine and Coastal Observing System Gloucester Point continuous water quality monitoring station at Gloucester Point, VA (http://web2.vims.edu/vecos/Default.aspx), located within 150 meters from the experimental study site. Linear regression models were performed to assess the effect of temperature on duration of positive buoyancy and total time to decay to code 5. Due to low sample size and lack of sufficient replicates across species and size classes, the effect of turtle species or size on decomposition could not be assessed, but we did not observe any obvious, large differences in decomposition between individuals of different sizes or species were observed.

2.2 Drift study

To assess the effect of wind forcing on turtle drift, three types of drifters were used: turtle carcass drifters, bucket drifters and wood-foam turtle drifters (Figure 3; Table 2). Turtle carcass drifters were constructed from the remains of deceased stranded turtles collected by VAQS (Figure 3A). Prior to use, the turtle plastron and carapace were separated during necropsy (with head and flippers still attached) and internal organs were removed. The body cavity was then filled with insulating foam sealant spray and holes were drilled around the perimeter of the plastron and carapace pieces, which were reattached with heavy-duty zip ties and a thin 1.5 cm x 1.5 cm galvanized wire mesh on the underside of the carcass (Figure A2). The amount of foam was based on the size of the body cavity and the need to maintain positive buoyancy. When the turtle carcass drifter was floating, the majority of the shell was fully exposed with the apex of the carcass edge forming the waterline, consistent with the floating behavior of a fully bloated turtle carcass. A satellite-transmitting GPS receiver (Assetlink TrackPack transmitters) was mounted on a self-righting crab pot buoy that was attached to the turtle via a rope passing through its carapace (Figure A3). Although the impact of the buoy itself on carcass drift was not quantified, it was made as small as possible and separated from the carcass to minimize impact. The carcasses were stored prior to use in a freezer and were frozen at time of release.

The "bucket drifters" used in this study were very-near surface "Kathleen" drifters made from inverted 5-gallon plastic buckets with weights and floats inside so as to be mostly submerged when in water (Chen et al. 2009, Putman and Mansfield 2015) (Figure 3B; http://www.nefsc.noaa.gov/epd/ocean/MainPage/lob/driftdesign.html). These were designed to track near surface currents with movements relatively unaffected by wind. Of all the drifters launched, the buckets most closely represent the movements of water particles, thus providing an estimate of the near-surface current field to be compared with movements of the other two drifter types.

The wood-foam turtle drifters were constructed out of layers of wood and polystyrene foam in the approximate form of a juvenile loggerhead sea turtle (Figure 3C). These drifters were included as a potential (more readily available) alternative to true turtle carcass drifters, although it is worthwhile to note that the aspect ratio of the wood-foam drifter was a bit higher than the turtle carcass drifters (e.g. whereas the difference between straight carapace length and curved carapace length for the carcass drifters ranged 5.2-7.8 cm, wood-foam drifters had a difference of 14.9 cm; Table 2). Additionally, the vertical profile of the wood-form turtle included steps whereas the profile of a true turtle carcass is rounded. Both bucket drifters and wood-foam turtle drifters were painted orange and small orange construction flags were attached on top to make the drifters more visible to boaters.

We conducted four drifter releases in the main stem of the lower Chesapeake Bay during the summer of 2016 (Figure 1A; Table 3). Each deployment included two bucket drifters and two wood-foam turtle drifters. Due to the limited number of turtle carcasses available for this study, only three loggerhead turtle carcasses were used in total. The first trial included two different carcasses, while the others used a third carcass, which was collected within 24 hours of beaching, refrozen, and redeployed for subsequent deployments. Given the large size of this third turtle carcass drifter, short deployment periods, and good initial carcass state, the multiple freeze-thaw cycles did not appear to compromise the head or flippers, all of which remained attached and essentially intact until the turtle was disposed of after the final deployment. The drifters were released by boat in the middle of the lower Chesapeake Bay and GPS locations were obtained every 30-minutes via satellite. Drifter positions were closely monitored until the objects beached, typically within 1-3 days.

Locations for all drifter types were matched in time by linearly interpolating between positions where necessary. Meteorological data (i.e., wind speed and direction) available in 6-minute intervals were obtained from the National Oceanographic and Atmospheric Administration's Center for Operational Oceanographic Products and Services (http://tidesandcurrents.noaa.gov/) monitoring station 8637611 York River East Rear Range

Light. Due to the presence of a weather front in the area during the second deployment, meteorological data for this trial were instead obtained from the 8638614 Willoughby Degaussing Station located in an adjacent tributary (Figures A4-A7). Wind speed was adjusted from 57 feet recorded height to the standard 10 m reference height using the methods described in Hsu et al. (1994). East-west (u) and north-south (v) wind vector components were computed and wind vector components were averaged over 30-minute intervals corresponding to the drifter data time series.

Drift leeway of the wood-foam drifters and turtle carcass drifters were computed based on the observed motion of the drifters relative to bucket drifters (most closely representing the surface current field). Leeway can be measured using a direct or indirect approach (Allen and Plourde 1999, Breivik et al. 2011). Here, drift leeway was measured indirectly by comparing the movements of the turtle and wood-foam drifters to those of the bucket drifters. The rate of change in the separation between drifters were calculated at pairs of consecutive time steps. Linear-regression analysis was used to derive leeway coefficients based on the slopes of the regression line between wind speed and along-wind leeway, cross-wind leeway or leeway speed. In addition, separation distances as a function of time since release were calculated between each combination of drifter pairs.

Due to the separation of drifters over time, movements were most comparable during the initial hours following deployment when objects were close together and likely experiencing the same physical oceanographic forces. Thus, the duration of each trial was limited from time of deployment to the next slack tide, when the tidal flow reversed direction and currents were weak and spatially incoherent (Hospital et al. 2015). This time period ranged from 2.5-8.5 hours based on deployment. Slack tide data were obtained from the National Oceanographic and

Atmospheric Administration's Tidal Current Predictions (http://tidesandcurrents.noaa.gov/) for station ACT5406 York River Entrance Channel (NW end).

Linear regression models used to estimate leeway coefficients for the turtle carcass drifters and wood-foam drifters included categorical variables for each deployment, (i.e. drifter release trial), turtle carcass drifter or wood-foam drifter, and the bucket being compared with a given carcass or wood-foam drifter trajectory. When estimating wood-foam drifter leeway, both bucket and wood-foam drifter were considered random nested effects inside wind speed and deployment. When estimating turtle carcass drifter leeway, bucket was a random effect nested inside wind speed, deployment and carcass drifter. The regression model included effects of categorical variables on both the intercept and slope of the relationship between wind speed and leeway. Analysis of variance was used to test for differences in wind leeway with deployment or individual carcass drifter.

Simple linear models including only wind speed as a predictor of leeway (values for which were averaged across buckets) were also run to calculate leeway coefficients for each deployment and turtle carcass drifter or wood-foam drifter combination. Both unconstrained (i.e., with a freely varying y-intercept) and constrained (i.e., y-intercept=0) linear regressions were performed. Note that p-values for constrained regression estimates are not reported because level of significance is unreliable when forcing the slope through zero.

2.3 Particle modeling

Estimated model parameters attained from the decomposition and drifter studies (i.e., likely drift duration from mortality location to stranding and along-wind leeway coefficient) were integrated into an oceanographic drift model simulating carcass drift trajectories in the Chesapeake Bay to observed stranding times and locations. The basic simulation strategy was to “release” many surface pseudo-particles (i.e., simulated particles) throughout the domain of the oceanographic model, track these for a period of time based on wind and current estimates from atmospheric and ocean circulation models, and identify those pseudo-particles that arrived at stranding zones for each month. The initial release points for many such “stranding” forward drift trajectories were then aggregated to estimate a probability distribution for the mortality locations of stranded turtles for June, the peak month for strandings. No additional randomness was added to the model to account for sub-grid-scale variability as the oceanographic and atmospheric models themselves have errors and uncertainties that would be difficult to quantify separately from sub-grid-scale variability.

Using ocean circulation data from a Regional Ocean Modeling System (ROMS; version 3.6) physical oceanographic model of the Chesapeake Bay area (ChesROMS; Feng et al. 2015), particles were released throughout the Bay and run forward in time using the offline Lagrangian drift simulation tool Ichthyop version 3.1 (Lett et al. 2008). Simulations were conducted for the time period 2001-2005 as ChesROMS ocean currents simulation data were only available for this period at the time of this study. Computer simulations were configured to release 1,000 particles randomly throughout the Bay every 6-hours with particle tracking time ranging from 2-8 days based on results from the decomposition study. Based on observed variability in along-wind leeway results from the drifter experiment, leeway ranging from 0-4% of wind speed were added to ChesROMS currents so that pseudo-particle trajectories represent the combined effects of currents and direct wind forcing on surface transport. Wind forcing was derived from the North American Regional Reanalysis (NARR) dataset (Mesinger et al. 2006). ChesROMS, NARR and Ichthyop internal timesteps were all 3 hours. NARR winds were unavailable for 2016 at the time of the study, and thus we were unable to use them for analyses in the drifter experiments.

Sea turtle stranding data collected by the Virginia Institute of Marine Science and VAQS during 2001-2005 were analyzed to identify areas with high numbers of strandings. The years 2001-2005 was chosen to be consistent with simulations, but using a longer time period does not change the regions identified as having a high stranding rate. Target zones were created in sections of Accomack, Hampton, Norfolk, Northampton and Virginia Beach Counties (Figure 1A). Each zone has a 3-km offshore extent. Computer simulations were run targeting these specific stranding-hotspots. Simulation results for relative particle density of the origins of particles reaching target zones were mapped on a 5km x 5km square grid.

3. Results

3.1 Decomposition study

Initial assessments of all turtle carcasses indicated that the bodies were in good condition with no significant marks or lesions, with the exception of one vessel-strike turtle carcass (turtle 3). The three lacerations on the vessel strike turtle did not seem to have severally altered decomposition as results for this turtle carcass were consistent with those for the other carcasses. A summary of condition code criteria used to evaluate the carcasses can be found in Table 1 and preliminary measurements of all turtle carcasses used in the study is noted in Table 4. The majority of the turtles were a code 1 upon placement at the York River study site and sank immediately. Positive buoyancy due to the accumulation of decomposition gases occurred within the first two days in all carcasses. At time of surfacing, all turtle carcasses were observed with some degree of bloating and assessed with a condition code of 2. Turtles 2 and 8 began as an early code 2 and did not sink upon initial placement, but remained floating at the water surface.

The effect of temperature was found to be statistically significant on both the duration of positive buoyancy ($p<0.001$, $R^2 = 0.8605$) and time to reach total decay (code 5) ($p<0.001$, $R^2 = 0.8401$) (Figure 4A). Duration of positive buoyancy ranged from 2-15 days. By a late code 3, all turtle carcasses deteriorated to a point that the body was no longer intact enough to retain decomposition gases, causing the bodies to sink and remain at the bottom of the sea floor until reaching code 5. Duration of complete decomposition to code 5 ranged from 5-18 days (Figure 4B, Table 5). The eighth turtle, submerged in cooler water temperatures averaging 17^{o}C, did not exhibit the same level of tissue disintegration as observed in the warmer water decomposition trials (with average water temperatures of 20-29^{o}C). The remains from this turtle formed a mass of tissue by day 18, when the turtle reached an early code 5. Nearly all of the bones were detached from the undistinguishable mass of fat by day 20, yet the tissue remnants were observed to persist until day 23, when all remains were lost through the mesh.

Occasional observations were made of organisms scavenging within the body cavity of the turtle carcasses during sampling, including juvenile blue crabs (*Callinectes sapidus*) and mud snails (*Nassarius spp*.) In addition, a Go-Pro camera attached to the decomposition set up of two trials (turtles 3 and 4) depicted the presence of a school of fish (*Menidia menidia)* feeding on the plastron-side of turtle 3 while it was floating at the surface.

3.2 Drift study

Wind speed, deployment and individual turtle carcass drifter were found to have a significant effect on along-wind leeway ($p>0.05$). Therefore, we conducted separate regressions for each deployment-turtle combination. Unconstrained regressions indicated that along-wind leeway was significantly related to wind speed for turtle carcass drifters 1 and 2, turtle carcass drifter 3 during deployment 3, and wood-foam drifters during deployments 1 and 3-4. Cross-wind leeway was not found to be significant for any turtle carcass drifter, but was significant for most of the wood-foam drifter deployments (Figure 5; Table 6). The 95% confidence interval of the slope for all components of leeway were largest in deployment 1 for both the turtle carcass drifters and wood-foam drifters, which was also the deployment trial of the longest duration.

Along-wind leeway coefficients from a constrained (i.e. y-intercept=0) linear regression ranged from 1.14-3.59% of wind speed, in wind conditions ranging from 0.08-4.24 m/s. At an average wind speed of 2.85 m/s, this equates to a change in carcass movements of 0.03-0.1 m/s due to the influence of wind versus currents alone. The along-wind leeway of the wooden turtles ranged from 0.73-3.54% of wind, equating to approximately a 0.02-0.1 m/s change in movement. Along-wind leeway coefficients for turtle carcass drifters and wood-foam drifters were positively correlated, but this correlation was not statistically different from zero (Pearson's correlation coefficient=0.73, p=0.17 for n=5).

Despite being released in nearby areas, the tracks of the drift objects varied significantly across deployments (Figure 6). Upon release, drifters were noted to diverge by type fairly quickly (<1 hour), but all continued to move in the same general direction following deployment until the direction of tidal currents began to reverse. This trend is most clearly observed in the drifter tracks during deployment 2, which was the shortest deployment with objects beaching approximately 26 hours after release. The buckets in particular were noted to remain fairly close to one another throughout the majority of the drift release trials, and were the last objects to make landfall in nearly all of the deployments.

3.3 Carcass drift simulations

During 2001-2005, 1487 of the reported Virginia sea turtle strandings occurred within the model domain. The vast majority of these strandings (82%, n=1222) occurred in three coastal areas of three Virginia counties: Northampton, Virginia Beach, and Norfolk (Figure 1A). Although stranding events took place throughout the spring and into the early fall, the majority of strandings occurred during late spring (May-June) and summer (Lutcavage and Musick 1985, Mansfield 2006, Barco and Swingle 2014), with nearly half of the standing events occurring during June alone (44%, n=660; Figure 1B).

The spatial distribution of location of mortality to these three top stranding zones were predicted using computer simulations applying a variety of parameter estimates covering the range of values identified in the drifter and decomposition studies. Along-wind leeway coefficients of 0%, 2% and 4% of wind speed were examined. Water temperatures in the lower Chesapeake Bay during peak times of late spring and summer strandings typically average around 20-30^{o}C, thus drift durations of 2, 5 and 8 days were examined. Summaries of release points of particles that land in the three top zones where Virginia strandings occur during the month of June suggest that most mortalities likely originate from areas within the lower Bay, including the waters near the entrance to the Bay and the James River, as well as coastal waters off of Virginia Beach county (Figures 7 and 8). An increase in drift duration was noted to increase the distance of particle origin from the zone in all cases but one (4% leeway for zone 2 for 8 days) (Table 7). Increasing the percentage of winds consistently increased distance of particle origin from the zone for 2 days drift, but results were mixed for longer drift periods. In addition, the total number of particles making landfall increased with increasing wind forcing values across all zones, regardless of drift duration. For example, there was at least a 50% increase in the absolute number of particles reaching Zone 1 in simulations with a wind forcing value of 4% versus 0% for all drift duration values (Figure A8).

In the lower Chesapeake Bay, prevailing winds exhibit seasonal variability, with winds prevailing from the southwest during the summer months (Paraso and Valle-Levinson 1996). Summertime probability maps of particle origins reflect these dominant wind patterns, with a notable shift towards a more eastern origin with the addition of stronger wind forcing, while a north-south shift was less consistent (Figure A9).

4. Discussion

To our knowledge, our study provides the first use of extensive field experimentation to better resolve key uncertainties when modeling dead turtle drift patterns, namely, water drift time before stranding and the influence of direct wind forcing on turtle carcass drift trajectories. Model simulations of top stranding zones throughout the Chesapeake Bay with different time and wind forcing parameters highlight the sensitivity of drift patterns to parameter estimates. This research is also the first efforts to use oceanographic modeling to identify potential areas of turtle mortality in Virginia's waters.

4.1 Decomposition study

The post-mortem interval is a key element in forensic investigations. All eight turtle carcasses in this study decomposed to bones in less than 18 days, in water temperatures averaging 17-29^{o}C. Higgins et al. (1995) observed the complete decay of two Kemp's ridley turtles from code 1 to code 5 in 4-12 days depending on water temperature, consistent with our results. These results also fit well within the range of decomposition for other aquatic animals, including an estimated drift duration for small cetaceans of 5-10 days depending on carcass state (Peltier et al. 2012).

The duration of carcass buoyancy is a key element to consider when interpreting stranding patterns. Only bloated, gas-filled carcasses with positive buoyancy can float and drift large distances. Thus, the probability of a particular turtle carcass making landfall is directly related to its buoyancy (Peltier et al. 2012). Water temperature plays a key role in the carcass surfacing time of deceased marine animals (Parker 1970, Higgins et al. 1995, Patterson et al. 2007, Peltier et al. 2012). Decay processes are initiated predominately by the activity of intestinal bacteria, which is accelerated in warmer conditions (Reisdorf et al. 2012). In this study, time period to attain buoyancy ranged from less than 24-hours in warmer water temperatures (28-29.5^{o}C) to 2-days in cooler waters (17.5-20.5^{o}C). Water pressure and depth can also influence carcass surfacing time, and thus decomposition rates in the shallow waters of this study may not be fully indicative of processes in deeper parts of the Bay. It is also worthwhile to note that the carcasses in this study were frozen prior to use. Studies have shown that previously frozen animals exhibit accelerated rates of disarticulation on land (Micozzi 1986), suggesting that duration to achieve buoyancy might be greater for fresh dead turtles compared to the frozen carcasses used in our study. Nonetheless, results match relatively well with Higgins et al. (1995), where fresh dead turtle carcasses surfaced in less than 24 hours after placement in 33-34^{o}C waters, and after 4-5 days in 14-22^{o}C waters. Sis and Landry (1992) observed red-eared pond slider carcasses to resurface in less than two days after postmortem, and some cetacean carcasses have been observed to inflate with gases within hours (Reisdorf et al. 2012). Although it is possible that bottom currents may transport carcasses from initial site of mortality, low current velocities in the bottom boundary layer, as well as contact with bottom sediments, likely lead to submerged carcasses not moving far before achieving positive buoyancy. For example, net displacement of a freshly deceased turtle prior to gaining buoyancy observed by Nero et al. 2013 was approximately 1-km over a submergence period of 4.8 days. Finally, a stratified water column with considerably lower temperatures at the bottom (e.g., as is typical of late spring) may slow decomposition processes at the bottom and thus increase the amount of time before a carcass surfaces beyond what was observed in our shallow water study.

Once a carcass surfaces, assuming it is not entangled, it will drift at the surface while continuing to gradually decompose (Reisdorf et al. 2012). The carcass will eventually decompose to a point where it is no longer intact enough to retain gases, and it will sink to the bottom of the sea floor. Thus, drift duration of carcasses is limited to only the interval of positive buoyancy, which varied with water temperature from 2 to 15 days in this study. In all trials, code 3 was the stage at which the carcasses were not intact enough to retain gases, thereby sinking and never reappearing again at the surface. These results are similar to those reported in Higgins et al. (1995), and suggests that stranded sea turtles found on beaches must land prior to reaching a late code 3. For stranded turtles found in condition code 4 or 5, it is probable that this level of decomposition occurred while on land or after reaching a shallow, nearshore environment. Uncertainty in the time component surrounding sea turtle decomposition on land can be limited by focusing on stranding events in highly populated areas, where beaches are frequently visited and strandings are likely reported and documented in a timely fashion.

Our results indicate that water temperature plays a significant role on the duration of surface drift time and thus on the probability of turtle carcasses making landfall. In particular, the timing of the annual spring peak of turtle strandings observed in the Chesapeake Bay during May and June may be partially explained by climatic conditions. Typically, sea turtles first begin entering the Chesapeake Bay around mid-May when water temperatures approach 18-20^{o}C (Mansfield 2006, Mansfield et al. 2009). Based on the results of this study, if mortality occurs at this time of the year when water temperatures are cooler, it is possible that turtles can drift for upwards of 15 days after surfacing. However, as the summer progresses and water temperatures rise, carcasses will likely decompose faster and thus drift for a much shorter time period (2-5 days). Therefore, increasing water temperature may decrease the likelihood of turtle carcasses beaching. Due to faster decomposition in warmer waters, it is also likely that from late summer to early fall only turtles that die close to shore will beach, as turtles dying further offshore will decompose before washing ashore.

4.2 Drift study

Our leeway drift estimates of turtle carcass drifters are among the first attempts to parameterize the drift characteristics of deceased sea turtles prior to stranding (but see Nero et al. 2013 for another recent attempt). We found that turtle carcasses drift at approximately 1.14-3.59% of the wind speed, equating to a change in movement of roughly 0.03-0.1 m/s based on typical Bay winds. With the typical currents in the Chesapeake Bay ranging from 0.1-0.2 m/s (Guo and Valle-Levinson 2007), the effect of wind on turtle carcass drift is non-negligible and must be considered when attempting to model drift trajectories.

Our use of constrained linear regressions (i.e., forcing the line of best fit to pass through the origin) should provide a more accurate estimate of leeway than an unconstrained regression assuming that objects remain at rest relative to surrounding waters in the absence of winds (Allen 2005, Breivik et al. 2011). It is also preferred over the unconstrained method when the range of wind speed is limited (Breivik et al. 2011). Notably, winds during the second deployment, for which relationships between along-wind leeway and wind speed were not significant, were the weakest and smallest in range of all deployments (Tables 3 and 6).

Our results of turtle drift between 1% and 4% of wind speed are similar to those reported for other drifting animals. The drift speed of sea birds and dolphins has been estimated to range between 2.5% and 4% of wind speed (Bibby and Lloyd 1977, Peltier et al. 2012), and Nero et al. (2013) estimated the drift leeway of a Kemp's ridley at 3.5% of wind from comparing the track of a satellite-tagged moribund turtle to simulated tracks from an ocean circulation model. Although the high aspect ratio of the wood-foam drifters may have contributed to the somewhat higher leeway values compared to the carcass drifters, the along-wind leeway for wood-foam drifters was similar in magnitude to that of turtle carcass drifters, ranging from 0.73-3.54%, suggesting that these artificial drifters may provide a good proxy for true turtle carcasses.

Given the limited number of turtle carcasses that were available to use for the drifter experiment, we cannot definitively say to what extent environmental variability between deployments and/or physical differences between turtles explain variability in along-wind leeway coefficient estimates. Nevertheless, there are suggestions in our data that both play a role. There was a positive correlation between turtle carcass drifters and wood-foam drifter leeway coefficients, suggestive of environmental differences between deployments being a source of leeway variability (because the same wood-foam drifters were used for all deployments, but carcasses differed between deployments). However, this correlation was not significantly different from zero, indicating that more data are needed to confirm this effect. Turtle size also appears to be related to leeway coefficient, but this effect is confounded with that of deployment, complicating a definitive assessment. Estimated along-wind leeway for the largest turtle carcass drifter (Carcass 2), which was used exclusively in the first deployment, was 3.59%, whereas for the smallest turtle carcass drifter (Carcass 3, used in deployments 2-4) it ranged from 1.14-

1.44%. This would suggest that larger carcasses are more heavily impacted by direct wind forcing, but again more data is needed to confirm this.

One study limitation was the limited temporal extent of leeway data due to the fast separation rate between the bucket drifters and the drift objects of interest. Here, we indirectly measured the leeway of the turtle objects by tracking its drift relative to the movements of the nearby bucket drifters, which were assumed to be representative of current conditions at the location of the turtle carcass drifter. However, this method is only effective when drifting objects are close together and in a relatively homogeneous current field, which typically only occurred over the first phase of the tidal cycle after deployment (within 5-8 hours of release). The direct method for estimating leeway coefficients, which uses a current meter attached directly to the drift object of interest, is another approach that can improve accuracy of leeway estimates (Breivik et al. 2011). In this study, the direct method was impractical due to the generally large size of current meters and/or expense of implementation. If the drift object is too small to tow a current meter, current data must be derived by some other means and thus the indirect method must be used (Breivik et al. 2011).

Future investigations should also consider the ratio of the carcass drifter’s above water to below water cross sectional area. Percent exposure is important in measurements of leeway (Isobe et al. 2011) and a better understanding of percent exposure of the carcass drifters is an important avenue for additional research into leeway variability in turtle carcasses. Nevertheless, the rough consistency of our results with the few other available leeway measurements in turtles and other marine species suggests that our results are not a gross misrepresentation of reality.

4.3 Carcass drift simulations

Probability maps for starting points of stranding pseudo-particles for the three zones with the highest number of strandings in Virginia's waters during the peak stranding month of June highlight areas of the lower Bay and coastal waters immediately south of the Bay mouth as hotspots for turtle mortality in the region (Figure 8). Although the majority of area strandings wash up on the lower bayside coast of Northampton County (Zone 1), our model suggests that mortality for most of these turtles occur in waters spanning across the entire lower Chesapeake Bay channel to the vicinity of the James River mouth. These lower Bay waters, particularly near the entrance of the James, are also highlighted as a mortality hotspot for turtles washing up on Norfolk and Virginia Beach coastlines (Zones 2 and 3), in addition to oceanic waters south of the Bay mouth. Even for relatively long summer drift periods of 8 days, most stranding particles originated within waters immediately east and west of the Bay mouth. The Chesapeake Bay and Virginia's coastal waters are subject to heavy commercial and recreational public use (Terwilliger and Musick 1995), thus sea turtles in these areas are likely often subject to interactions with human activities. Although cause of death for a vast number of Virginia strandings cannot be determined from visual assessment or necropsies alone (Lutcavage and Musick 1985), results of this study provide focus areas for further investigations of potential causal mechanisms of mortality.

In addition, simulation results indicate the importance of physical processes and decomposition rates for accurately estimating mortality locations. The mean location of particle origin prior to beaching was noted to move further offshore as drift duration increased (Table 7), consistent with studies that demonstrate a negative correlation between release distance and carcass recovery (Hart et al. 2006). Importantly, this also highlights a probable bias in stranding records. Although simulation results depict the majority of turtles as dying relatively close to stranding locations, this may not reveal a lack of turtle mortality further offshore, but rather that dead turtles have a greater likelihood of making landfall if mortality occurs closer to shore and in areas with high coastal retention (otherwise their bodies may simply be lost at sea). For example, the area off the bayside coast of southern Northampton County (Zone 1) where the most strandings and particle retention occurred is also the area of a cyclonic eddy system which has been noted to entrain particles in other studies (Hood et al. 1999). The high number of strandings observed in this area may be due to prevailing physical processes facilitating the entrainment of carcasses, further highlighting the key role physical oceanographic processes play in determining the likelihood that a sea turtle carcass strands. Improving representation of sub-grid-scale variability in the carcass drift model could increase the spread of particles and represents a possible improvement for future modeling studies.

Increasing the along-wind leeway coefficient used in the model had variable effects (depending on duration of drift period) on the distance from the target zones and spatial spread of probable points of origin for stranding particles. Nevertheless, increasing this parameter consistently increased the number of particles making landfall for all target zones (Figure A8). As currents move predominantly in an alongshore direction, the addition of winds allows for cross-shore movement of simulated particles, facilitating deposition in coastal areas. These trends were also reflected in the drift deployment experiments. The bucket drifters were the last objects to make landfall in nearly all of the deployments, highlighting the essential need to incorporate wind forcing effects in oceanographic simulations to properly represent drift of deceased turtles.

4.4 Conclusion

Although sea turtle strandings provide a unique opportunity to study turtle mortality, these events often provide little insight on causes of mortality and likely only represent a fraction of total mortality occurring at sea. Given the protected status of sea turtles, availability of turtle carcasses for research to elucidate drift patterns of turtle carcasses is extremely limited. Despite the limited sample size, our results provide the best estimate of turtle drift parameters currently available, and therefore, have significant potential for future use in modeling simulations aimed at interpreting stranding data. For example, the Sea Turtle Stranding and Salvage Network has been monitoring and collecting data on turtle strandings in the United States since 1980. With a dataset spanning several states and more than 30 years, this data potentially provides an important opportunity to apply our model to strandings in other geographic regions. Hindcasts of turtle carcass drift trajectories to final terrestrial stranding locations can be extremely useful in interpreting stranding events, and accurate information on the drift characteristics of sea turtles will result in more precise predictions of potential mortality locations.

This work is an important step for more robust analyses modeling the drift of stranded sea turtles to Chesapeake Bay beaches. Furthermore, drift information obtained from this study can be utilized in sea turtle carcass drift models to analyze strandings data from many other areas of the world. Our results indicate that sea turtle drift time may be quite short at 2-15 day in typical Bay spring-early fall conditions. We also determined that turtles drift at 1-4% of wind speed, demonstrating that direct wind forcing has a non-negligible role in determining drift trajectories. Oceanographic simulations identify potential mortality hotspots for the peak month of strandings (June) in waters of the lower Chesapeake Bay and oceanic areas off southern Virginia, providing focus areas for future investigations into likely drivers of sea turtle mortality.

These results are essential to improving our ability to predict mortality locations from stranding events not only in the Chesapeake Bay, but around the globe, providing managers with essential information to better protect vulnerable sea turtle populations worldwide.

Acknowledgments

We would like to acknowledge the Virginia Aquarium & Marine Science Center Stranding Response Program and A. Weschler with the Maryland Department of Natural Resources for providing the sea turtle carcasses used in this study. We would also like to thank J. Gwartney-Green, S. Rollins, J. Snouck-Hurgronje, T. Armstrong, D. Jones, and K. Bemis for assistance in the field and S. Rollins and D. Malmquist for providing photos. Funding for this project was provided through the College of William and Mary's Green Fee Funding, the Virginia Institute of Marine Science (VIMS), the VIMS GK-12 Sheldon H. Short Trust Program, the Dominion Foundation and Virginia Sea Grant. This work was performed in part using computational facilities at the College of William and Mary which were provided with the assistance of the National Science Foundation, the Virginia Port Authority, Sun Microsystems, and Virginia's Commonwealth Technology Research Fund. Mention of trade names is for identification purposes only and does not imply endorsement the National Oceanic and Atmospheric Administration nor any of its subagencies. We thank two anonymous reviewers for their constructive and encouraging comments that greatly improved this manuscript. This is contribution XXXX from the Virginia Institute of Marine Science.

Literature Cited

Allen, A. 2005. Leeway Divergence. Technical Report No. CG-D-05-05, U.S. Coast Guard Research and Development Center. Groton, CT.

Allen, A. A., and J. V. Plourde. 1999. Review of Leeway: Field Experiments and Implementation. Technical Report No. CG-D-14-98, U.S. Coast Guard Research and Development Center. Groton, CT.

Barco, S., and W. M. Swingle. 2014. Sea Turtle Species in the Coastal Waters of Virginia: Analysis of stranding and survey data. VAQF Scientific Report #2014-07b, Virginia Aquarium & Marine Science Center Foundation. Virginia Beach, VA.

Bellmund, S., J. A. Musick, R. Klinger, R. Byles, J. A. Keinath, and D. Barnard. 1987. Ecology of sea turtles in Virginia. Scientific Report No. 119, Virginia Institute of Marine Science. Gloucester Point, VA.

Bibby, C. J. 1981. An Experiment on the Recovery of Dead Birds from the North Sea. Ornis Scandinavica 12:291–265.

Bibby, C. J., and C. S. Lloyd. 1977. Experiments to determine the fate of dead birds at sea. Biological Conservation 12:295–309.

Breivik, O., A. A. Allen, C. Maisondieu, and J. C. Roth. 2011. Wind-induced drift of objects at sea: The leeway field method. Applied Ocean Research 33:100–109.

Chen, F., D. G. MacDonald, and R. D. Hetland. 2009. Lateral spreading of a near-field river plume: Observations and numerical simulations. Journal of Geophysical Research 114:C07013.

Coles, W. C. 1999. Aspects of the Biology of Sea Turtles in the Mid-Atlantic Bight. PhD Dissertation, Virginia Institute of Marine Science, College of William and Mary. Gloucester Point, VA.

Dealteris, J., and R. Silva. 2007. Performance in 2004 and 2005 of an alternative leader design on the bycatch of sea turtles and the catch of finfish in Chesapeake Bay pound nets, offshore Kiptopeake, VA. National Marine Fisheries Service, New England Fisheries Science Center. Woods Hole, MA.

Degange, A. R., A. Doroff, and D. H. Monson. 1994. Experimental recovery of sea otter carcasses at Kodiak Island, Alaska, following the Exxon Valdez oil spill. Marine Mammal Science 10:492–496.

Epperly, S. P., J. Braun, A. J. Chester, F. A. Cross, J. V Merriner, P. A. Tester, and J. H. Churchill. 1996. Beach strandings as an indicator of at-sea mortality of sea turtles. Bulletin of Marine Science 59:289–297.

Feng, Y., M. A. M. Friedrichs, J. Wilkin, H. Tian, Q. Yang, E. E. Hofmann, J. D. Wiggert, and R. R. Hood. 2015. Chesapeake Bay nitrogen fluxes derived from a land-estuarine ocean biogeochemical modeling system: Model description, evaluation, and nitrogen budgets. Journal of Geophysical Research: Biogeosciences 120:1666–1695.

Guo, X., and A. Valle-Levinson. 2007. Tidal effects on estuarine circulation and outflow plume in the Chesapeake Bay. Continental Shelf Research 27:20–42.

Hart, K. M., P. Mooreside, and L. B. Crowder. 2006. Interpreting the spatio-temporal patterns of sea turtle strandings: going with the flow. Biological Conservation 129:283–290.

Higgins, B., A. Cannon, and G. Gitschlag. 1995. Sea turtle decomposition study. Unpublished report, National Marine Fisheries Service, Southeast Fisheries Science Center. Galveston, TX.

Hood, R. R., H. V. Wang, J. E. Purcell, E. D. Houde, and L. W. Harding. 1999. Modeling particles and pelagic organisms in Chesapeake Bay: Convergent features control plankton distributions. Journal of Geophysical Research 104:1223.

Hospital, A., J. A. Stronach, M. W. McCarthy, and M. Johncox. 2015. Spill response evaluation using an oil spill model. Aquatic Procedia 3:2–14.

Hsu, S. A., E. A. Meindl, and D. B. Gilhousen. 1994. Determining the power-law wind-profile exponent under near-neutral stability conditions at sea. Journal of Applied Meteorology 33:757-765.

Koch, V., H. Peckham, A. Mancini, and T. Eguchi. 2013. Estimating at-sea mortality of marine turtles from stranding frequencies and drifter experiments. PloS one 8:e56776.

Lett, C., P. Verley, C. Mullon, C. Parada, T. Brochier, P. Penven, and B. Blanke. 2008. A Lagrangian tool for modelling ichthyoplankton dynamics. Environmental Modelling & Software 23:1210–1214.

Lutcavage, M., and J. A. Musick. 1985. Aspects of the biology of sea turtles in Virginia. Copeia 1985:449–456.

Mansfield, K. L. 2006. Sources of mortality, movements and behavior of sea turtles in Virginia. PhD Dissertation, Virginia Institute of Marine Science, College of William & Mary. Gloucester Point, VA.

Mansfield, K. L., V. S. Saba, J. A. Keinath, and J. A. Musick. 2009. Satellite tracking reveals a dichotomy in migration strategies among juvenile loggerhead turtles in the Northwest Atlantic. Marine Biology 156:2555–2570.

Mesinger, F., G. DiMego, E. Kalnay, K. Mitchell, P. C. Shafran, W. Ebisuzaki, D. Jović, J. Woollen, E. Rogers, E. H. Berbery, M. B. Ek, Y. Fan, R. Grumbine, W. Higgins, H. Li, Y. Lin, G. Manikin, D. Parrish, W. Shi, F. Mesinger, G. DiMego, E. Kalnay, K. Mitchell, P. C. Shafran, W. Ebisuzaki, D. Jović, J. Woollen, E. Rogers, E. H. Berbery, M. B. Ek, Y. Fan, R. Grumbine, W. Higgins, H. Li, Y. Lin, G. Manikin, D. Parrish, and W. Shi. 2006. North American Regional Reanalysis. Bulletin of the American Meteorological Society 87:343–360.

Micozzi, M. S. 1986. Experimental study of postmortem change under field conditions: effects of freezing, thawing, and mechanical injury. Journal of forensic sciences 31:953–961.

Murphy, T. M., and S. R. Hopkins-Murphy. 1989. Sea Turtle and Shrimping Interactions: A Summary and Critique of Relevant Information. Center for Marine Conservation. Washington, DC.

Musick, J. A., and C. J. Limpus. 1997. Habitat utilization and migration in juvenile sea turtles. Pages 137–163 in P. L. Lutz and J. A. Musick, editors. The biology of sea turtles. CRC Press, Boca Rouge, FL.

National Marine Fisheries Service. 2006. Sea Turtle Conservation; Modification to Fishing Activities. Federal Register 71:36024-36033.

National Research Council. 1990. Decline of the Sea Turtles: Causes and Prevention. Committee on Sea Turtle Conservation. National Academy Press, Washington, D.C:255.

Nero, R. W., M. Cook, A. T. Coleman, M. Solangi, and R. Hardy. 2013. Using an ocean model to predict likely drift tracks of sea turtle carcasses in the north central Gulf of Mexico. Endangered Species Research 21:191–203.

Paraso, M. C., and A. Valle-Levinson. 1996. Meteorological Influences on Sea Level and Water Temperature in the Lower Chesapeake Bay: 1992. Estuaries 19:548–561.

Parker, J. R. O. 1970. Surfacing of dead fish following application of rotenone. Transactions of the American Fisheries Society 99:805–807.

Patterson, D. A., K. M. Skibo, D. P. Barnes, J. A. Hills, and J. S. Macdonald. 2007. The influence of water temperature on time to surface for adult sockeye salmon carcasses and the limitations in estimating salmon carcasses in the Fraser River , British Columbia. North American Journal of Fisheries Management 27:37–41.

Peltier, H., W. Dabin, P. Daniel, O. Van Canneyt, G. Dorémus, M. Huon, and V. Ridoux. 2012. The significance of stranding data as indicators of cetacean populations at sea: Modelling the drift of cetacean carcasses. Ecological Indicators 18:278–290.

Putman, N. F., and K. L. Mansfield. 2015. Direct Evidence of Swimming Demonstrates Active Dispersal in the Sea Turtle “Lost Years”. Current Biology 25:1–7.

Reisdorf, A. G., R. Bux, D. Wyler, M. Benecke, C. Klug, M. W. Maisch, P. Fornaro, and A. Wetzel. 2012. Float, explode or sink: postmortem fate of lung-breathing marine vertebrates. Palaeobiodiversity and Palaeoenvironments 92:67–81.

Sis, R. F., and A. M. Landry. 1992. Postmortem Changes in the Turtle. Proceedings of the 23rd Annual International Association for Aquatic Animal Medicine, Hong Kong, pp. 17-19. San Leandro, CA.

Swingle, W. M., M. C. Lynott, E. B. Bates, L. R. D'Eri, G. G. Lockhart, K. M. Phillips, and M. D. Thomas. 2016. Virginia Sea Turtle and Marine Mammal Stranding Network 2015 Grant Report. Final Report to the Virginia Coastal Zone Management Program, NOAA CZM Grant #NA14NOS4190141, Task 49. VAQF Scientific Report 2016-01. Virginia Beach, VA.

Terwilliger, K., and J.A. Musick (co-chairs), Virginia Sea Turtle and Marine Mammal Conservation Team. 1995. Management Plan for Sea Turtles and Marine Mammals in Virginia, Final Report to the National Oceanic and Atmospheric Administration. 56 pp.

Turtle Expert Working Group. 1998. An Assessment of the Kemp's Ridley (Lepidochelys kempii) and loggerhead (Caretta caretta) Sea Turtle Populations in the Western North Atlantic. NOAA Technical Memorandum NMFS-SEFSC-409. 96 pp.

Wyneken, J. 2001. The anatomy of sea turtles. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-SEFSC 470. 172 pp.

Tables

Table 1. Summary of condition code criteria. Descriptions are compiled from observations noted during the sea turtle decomposition study and the National Oceanographic and Atmospheric Administration's Sea Turtle Stranding Salvage Network stranding report forms and guidelines (http://www.sefsc.noaa.gov/species/turtles/strandings.htm).

Condition Code	Carcass State	Criteria
0	Alive	
1	Fresh dead	No odor, scutes and skin intact, no bloating, turtle may still be in rigor
2	Moderately decomposed	Mild to strong odor, slightly to very bloated, body mostly intact with skin and scutes only beginning to peel, some small cuts/scratches, internal organs still distinguishable
3	Severely decomposed	Carcass deflated, strong to no odor, moderate to significant amount of skin peeling, internal organs beginning to liquefy, hard to distinguish individual organs, large abrasions on body cavity
5	Skeleton, bones only	Carapace and plastron no longer held together, any soft tissue remains are minimal and unidentifiable, bones are clean or have minimal attached tissues

Table 2. Summary of drifter measurements. Turtle curved carapace length (CCL) and straight carapace length (SCL) measurements were taken from notch to tip. Asterisks (*) represents an estimated measurement due to the presence of epibiota.

Drifter type	Size (cm)
Bucket drifter	Height: 36.0 Diameter (bottom): 26.0
Wood-foam drifter	CCL: 88.5 SCL: 73.6
Turtle Carcass Drifter 1	CCL: 83.5* SCL: 76.7*
Turtle Carcass Drifter 2	CCL: 101.3* SCL: 93.5
Turtle Carcass Drifter 3	CCL: 72.5 SCL: 67.3

Table 3. Summary of drift deployments. The duration of the trial was established based on duration to slack tide, while the entire deployment was considered completed when the first object beached.

	Deployment 1	Deployment 2	Deployment 3	Deployment 4
Composition				
Number of Buckets	2	2	2	2
Number wood-foam drifters	2	2	2	2
Carcasses used	1, 2	3	3	3
Start of Deployment				
Location	37.17389, -76.2161	37.22833, -76.2161	37.22833, -76.1925	37.22232, -76.2328
Date	13-Jun-16	24-Jun-16	1-Aug-16	15-Aug-16
Time (GMT)	15:41	14:15	17:00	13:29
Water temperature (°C)	24.2	24.3	29.0	28.5
Air temperature (°C)	20.9	24.0	28.4	29.6
End of Trial				
Date	14-Jun-16	24-Jun-16	1-Aug-16	15-Aug-16
Time (GMT)	00:11	19:15	19:30	18:29
Duration (hh:mm)	8:30	5:00	2:30	5:00
10 m wind speed (m/s)	2.47 ± 0.79	2.37 ± 0.45	3.60 ± 0.55	2.73 ± 0.82
10 m wind speed range (m/s)	0.08-3.48	1.35-3.56	2.16-4.24	1.32-3.95
End of Deployment[a]				
Date	15-Jun-16	25-Jun-16	2-Aug-16	18-Aug-16[b]
Time (GMT)	16:30	16:50	15:13	5:22[b]
Duration (hh:mm)	48:49	26:35	22:13	63:53
10 m average wind speed	4.50 ± 1.38	3.67 ± 1.77	3.40 ± 0.86	3.76 ± 1.17
10 m wind speed range (m/s)	0.08-7.72	0.01-7.52	1.60-5.08	1.32-6.40

a. Deployment considered completed once first item beached
b. One of the buckets stopping emitting location data on 16-Aug-16 at 1:29 GMT

Table 4. Measurements of turtle carcasses used in the decomposition study.

Measurement (cm)	Turtle 1	Turtle 2	Turtle 3	Turtle 4	Turtle 5	Turtle 6	Turtle 7	Turtle 8
Species[a]	Cc	Cc	Cm	Lk	Cm	Cm	Cm	Lk
Weight (kg)	31.5	36.5	3.036	2.378	3.464	2.74	2.50	6.38
Straight carapace length (notch to tip)	68.0	67.2	29.3	26.3	30.4	28.6	28.9	37.4
Straight carapace width	54.0	54.3	22.8	23.9	24.2	23.3	22.9	32.6
Maximum head length	17.4	18.2	7.9	8.4	7.9	7.4	7.4	10.6
Body depth	23.1	24.2	11.6	8.8	11.7	10.6	10.2	15.3
Straight plastron length	46.5	52.6	25.7	20.2	24.9	23.6	23.3	27.8
Circumference at max width	112.8	125.0	53.3	54.0	55.3	51.6	49.9	75.4

a. Cc = *Caretta caretta*, Cm = *Chelonia mydas*, Lk = *Lepidochelys kempii*

Table 5. Summary of decomposition results for each turtle carcass.

Turtle No.	Species[a]	Study Dates		Temp (°C)	Days buoyant	Minimum days to reach condition code			
		Start	End			Code 1	Code 2	Code 3	Code 5
1	Cc	23-Jul-15	31-Jul-15	28.69±0.57	3	0	2	4	6
2	Cc	27-Aug-15	5-Sep-15	26.98±0.46	5	N/A[b]	0	3	5
3	Cm	14-Jun-16	22-Jun-16	24.32±0.56	5	0	2	4	7
4	Lk	20-Jun-16	28-Jun-16	24.62±0.82	4	0	2	5	7
5	Cm	28-Jul-16	2-Aug-16	29.54±0.61	2	0	1	3	4
6	Cm	2-Aug-16	7-Aug-16	28.55±0.41	2	0	1	3	5
7	Cm	11-Oct-16	24-Oct-16	20.37±1.24	8	0	2	6	12
8	Lk	24-Oct-16	15-Nov-16	17.03±2.62	15	N/A[b]	0	9	18

a. Cc = *Caretta caretta*, Cm = *Chelonia mydas*, Lk = *Lepidochelys kempii*

b. Turtles 2 & 8 began as an early code 2

Table 6. Unconstrained (i.e., with a freely varying y-intercept) and constrained (i.e., y-intercept=0) linear regression parameters, including the y-intercept (y-int.), slope, 95% confidence interval (C.I.), and significance (signif.), for the turtle carcass drifters and wood-foam drifters during each deployment (deploy.). Slope and standard error are represented as a percentage of wind speed. Level of significance of slope is represented by asterisks (.<0.1, *<0.05, **<0.01,***<0.001).

Along-wind component of leeway							
			Unconstrained			Constrained	
Drift object	Deploy.	Y-int.	Slope (%)	95% C.I. (%)	Signif.	Slope (%)	95% C.I. (%)
Turtle carcass drifter 1	1	-5.45	2.26	1.08-3.44	***	2.15	1.78-2.52
Turtle carcass drifter 2	1	15.72	3.26	0.85-5.67	**	3.59	2.84-4.35
Turtle carcass drifter 3	2	5.41	1.32	(-0.73)-3.37		1.44	1.13-1.76
	3	-103	2.76	0.98-4.54	*	1.14	0.83-1.44
	4	10.71	1.05	(-0.625)-2.73		1.25	0.83-1.68
Wood-foam drifters	1	-34.9	4.27	2.19-6.35	***	3.54	2.19-6.35
	2	2.94	0.66	(-1.23)-2.56		0.73	(-1.23)-2.55
	3	-59.57	2.90	0.85-4.93	*	1.95	0.85-4.93
	4	36.20	1.42	0.05-2.80	*	2.11	0.05-2.80
Cross-wind component of leeway							
			Unconstrained			Constrained	
Drift object		Y-int.	Slope (%)	95% CI (%)	Signif.	Slope (%)	95% CI (%)
Turtle carcass drifter 1	1	22.53	1.09	(-2.31)-4.49		1.56	0.50-2.63
Turtle carcass drifter 2	1	-48.92	1.34	(-1.54)-4.22		0.31	(-0.60)-1.22
Turtle carcass drifter 3	2	-20.34	0.89	(-3.25)-5.02		0.42	(-0.22)-1.05
	3	-51.31	2.94	(-1.23)-1.82		-0.52	(-0.72)-(-0.31)
	4	-28.90	2.76	(-0.76)-1.32		-0.27	(-0.54)-0.004
Wood-foam drifters	1	-11.99	3.30	0.43-6.17	*	3.05	2.14-3.95
	2	171.09	-3.40	(-5.47)-(-1.91)	***	0.25	(-0.12)-0.61
	3	-76.18	1.13	(-3.71)-5.96		-0.08	(-0.67)-0.52
	4	-78.08	1.26	0.09-2.42	*	-0.21	(-0.54)-0.12
Leeway speed							
			Unconstrained			Constrained	
Drift object		Y-int.	Slope (%)	95% CI (%)	Signif.	Slope (%)	95% CI (%)
Turtle carcass drifter 1	1	14.99	3.45	1.89-5.01	***	3.77	3.28-4.25
Turtle carcass drifter 2	1	138.01	1.53	(-0.24)-3.30	.	4.43	3.76-5.09

Turtle carcass drifter 3	2	23.16	1.39	(-0.18)-2.96	.	1.92	1.68-2.17
	3	-68.91	2.35	0.24-4.47	*	1.27	0.99-1.54
	4	16.90	1.14	(-0.28)-2.56		1.46	1.09-1.82
Wood-foam drifters	1	28.86	5.34	3.52-7.17	***	5.95	5.37-6.25
	2	51.05	0.21	(-1.05)-1.46		1.38	1.17-1.59
	3	-32.28	2.66	0.59-4.72	*	2.15	1.89-2.40
	4	52.25	1.38	0.15-2.61	*	2.37	2.03-2.70

Table 7. Mean distance (km) of particle origin 2, 5, and 8 days prior to landing in stranding zone under wind forcing conditions of 0%, 2%, and 4%. Results are compiled over 5 months of June from the years 2001-2005.

Mean distance from zone (km)									
Zone #	0% wind			2% wind			4% wind		
	2 days	5 days	8 days	2 days	5 days	8 days	2 days	5 days	8 days
1	9.78	21.80	33.77	12.14	18.34	23.36	14.35	19.12	22.35
2	10.63	24.62	37.34	11.41	19.45	23.50	14.71	22.66	22.23
3	9.47	17.82	26.95	12.86	19.36	22.79	17.05	21.87	24.33

Figure Legends

Figure 1. (A) Location of study sites within the Chesapeake Bay, VA, including the decomposition rate study (triangle), release points for the four drifter deployments (circles), and target zones for the oceanographic simulations (black outline). The target zones represent county-level areas which make up 95.5% of the reported 2001-2005 Virginia sea turtle strandings occurring within the model domain (n=1487). 82% of these strandings (n=1222) occur specifically within three zones (shaded in dark gray and numbered). (B) Total number of stranding events per zone (gray) and events occurring during June only (white; 44%, n=660) from the years 2001-2005. Stranding zone number corresponds to locations in Figure 1A, while "other" is composed of documented stranding events in the remaining outlined zones.

Figure 2. (A) Schematic of the decomposition study experimental design. (B) Image of a turtle carcass floating at sea. (C) Image of a turtle carcass on shore.

Figure 3. (A) Turtle carcass, (B) bucket, and (C) wood-foam drifters.

Figure 4. (A) Duration of positive buoyancy (circles, solid line) and time to total decay (triangles, dotted line) vs average water temperature (^{o}C). (B) Boxplot of the minimum number of days to reach each condition code stage.

Figure 5. Along-wind component of leeway (10^2 m/s), cross-wind component of leeway (10^2 m/s), and leeway speed vs. wind speed (10^2 m/s) for each turtle carcass drifter and wood-foam deployment. Values are averaged over half hour periods. Solid lines represent the unconstrained linear regression mean and the shaded polygon represents the 95% confidence intervals.

Figure 6. Complete drift tracks of all individual drifters during the four deployments.

Figure 7. Relative particle density (%) for probability of point of origin 2, 5 and 8 days prior to stranding in Zone 1, as outlined in blue. Results include 0%, 2% and 4% of direct wind forcing on carcass drift. Simulation results are a composite over 5 months of June for the years 2001-2005.

Figure 8. Relative particle density (%) for probability of point of origin 2, 5 and 8 days prior to stranding in outlined zone with 2% of direct wind forcing on carcass drift. Simulation results are a composite over 5 months of June for the years 2001-2005.

Appendix

Figure A1. Images of Turtle 1 at various condition code stages.

Figure A2. Schematic of sea turtle carcass drifter, including (A) carapace view, (B) plastron view, and (C) side-profile.

Figure A3. Self-righting buoy attachment with GPS for wood-foam and turtle carcass drifters.

Figure A4. NOAA National Weather Service daily weather map from July 24, 2016 depicting the presence of a weather front moving through the study site of deployment 2 (black box). Available from: http://www.wpc.ncep.noaa.gov/dailywxmap/index_20160624.html.

Figure A5. Locations of monitoring stations 8637611 York River East Rear Range Light (red circle), 8638614 Willoughby Degaussing Station (blue circle), and deployment 2 release location (yellow triangle).

Figure A6. Reported wind speed (m/s) and wind direction (degrees from true north) from monitoring stations 8637611 York River East Rear Range Light and 8638614 Willoughby Degaussing Station. Area between the blue lines represent the full time period of deployment 2.

Figure A7. Deployment 2 results of the along-wind component of leeway for turtle carcass drifter 3 using metrological data from monitoring stations (A) 8637611 York River East Rear Range Light and (B) 8638614 Willoughby Degaussing Station. Dashed lines represent 95% confidence intervals.

Figure A8. Relative number of particles from the oceanographic model making landfall over elapsed time (days). Simulation results are a composite over 5 months of June from the years 2001-2005.

Figure A9. Mean starting locations 2, 5, and 8 days prior to stranding in top zones. Simulation results are a composite over 5 months of June from the years 2001-2005.