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Integrating Empirical Data and Ocean Drift Models to Better Understand Sea Turtle Strandings in Virginia

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Integrating Empirical Data and Ocean Drift Models to Better Understand Sea Turtle
Strandings in Virginia

A Thesis

Presented to

The Faculty of the School of Marine Science

The College of William and Mary in Virginia

In Partial Fulfillment

of the Requirements for the Degree of

Master of Science


by

Bianca S. Santos

August 2017

APPROVAL PAGE

This thesis is submitted in partial fulfillment of
the requirements for the degree of
Master of Science




Bianca S. Santos

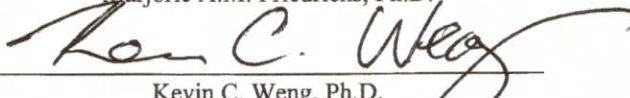
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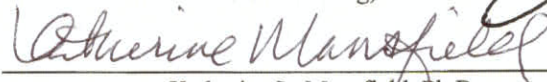
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DEDICATION

In loving memory of my father, João José Santos (1962-2004).

TABLE OF CONTENTS

ACKNOWLEDGEMENTS	iv
LIST OF TABLES	v
LIST OF FIGURES	vi
ABSTRACT	ix
INTRODUCTION	1
References	7
CHAPTER 1: CONSEQUENCES OF DRIFT AND CARCASS DECOMPOSITION IN ESTIMATING SEA TURTLE MORTALITY	
HOTSPOTS	10
Abstract	11
Introduction.....	12
Methods.....	15
Decomposition study	16
Drift study	18
Particle modeling	22
Results.....	23
Decomposition study	23
Drift study	25
Carcass drift simulations.....	26
Discussion	27
Decomposition study	28
Drift study	31
Carcass drift simulations.....	33
Conclusion	35
Acknowledgements.....	37
References.....	38
Tables	42
Figures.....	50
Appendix.....	58

CHAPTER 2: PROBABLE LOCATIONS OF SEA TURTLE
MORTALITY FROM STRANDINGS USING EXPERIMENTALLY-
CALIBRATED, TIME- AND SPACE-SPECIFIC CARCASS DRIFT

MODELS	67
Abstract	68
Introduction.....	69
Methods.....	73
Stranding data	74
Criteria for a “successful” stranded particle	75
Analyses	78
Results.....	82
Vessel strikes	83
No apparent injuries and unable to assess.....	84
Wind forcing.....	85
Fishing data.....	85
Discussion	86
Vessel strikes	87
Potential fisheries interactions	88
Mitigation measures.....	92
Conclusion	94
Acknowledgements.....	96
References.....	97
Tables.....	102
Figures.....	104
Appendix.....	114
CONCLUSION.....	117
References.....	123
VITA.....	124

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LIST OF TABLES

CHAPTER 1

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	42
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.....	43
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.....	44
4. Measurements of turtle carcasses used in the decomposition study.....	45
5. Summary of decomposition results for each turtle carcass.....	46
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 carcasses and wooden-Styrofoam turtles 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).....	47
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.....	49

CHAPTER 2

1. Criteria that must be met for each pseudo-particle to be considered “successful” for a particularly stranding event.	102
2. Linear regression parameters including the y-intercept (Y-int.), slope, and significance (signif.), from the decomposition study, relating temperature with minimum (min) and maximum (max) buoyancy times during condition codes 1-3. Level of significance of slope is represented by asterisks (<0.1, *<0.05, **<0.01,***<0.001).....	103

LIST OF FIGURES

CHAPTER 1

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). (B) Total number of stranding events per zone (gray) and events occurring during June only from the years 2001-2005	50
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.....	51
3. (A) Turtle carcass, (B) bucket, and (C) wood-Styrofoam drifters	52
4. (A) Duration of positive buoyancy (circles, solid line) and time to total decay (triangles, dotted line) vs average water temperature (°C). (B) Boxplot of the minimum number of days to reach each condition code stage.	53
5. (A) Along-wind component of leeway (m/s), (B) Cross-wind component of leeway (m/s), and (C) Leeway speed vs. wind speed (m/s) for each turtle carcass-deployment combination. Values are averaged over half hour periods. Solid lines represent the unconstrained linear regression mean and the shaded polygon represents the 95% confidence intervals.....	54
6. Complete drift tracks of all individual drifters during the four deployments.	55
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.....	56
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.....	57

CHAPTER 2

1. (A) Location of top three areas with reported sea turtle strandings in Virginia from 2009-2014, including 1) the bay-side of Northampton County, 2) Norfolk County, and 3) Virginia Beach County. (B) Expanded view of the lower Chesapeake Bay 104
2. Duration of positive buoyancy (days) vs average water temperature (°C) based on results from the experimental decomposition study..... 105
3. Boxplot of average (A) drift times (days) and (B) drift distances (km) of modeled particles leading to a condition code 3 stranding event. Results are aggregated by week of the year with gray-colored boxes representing strandings occurring during the spring peak time period. (C) Linear regression of drift time (days) vs drift distance (km)..... 106
4. (A) Vessel density (%). (B) Relative particle density (%) for probability of point of origin for turtle mortality leading to a stranding and classified with probable cause of death as vessel strike. (C) Combined joint probability (%) depicting the overlap between boating activity and the predicted mortality locations of vessel strike strandings... 107
5. Relative particle density (%) for probability of point of origin for turtle mortality leading to a stranding and classified with probable cause of death as no apparent injuries during (A) the spring peak and (B) the remainder of the stranding period..... 108
6. Relative particle density (%) for probability of point of origin for turtle mortality leading to a stranding and classified with probable cause of death as unable to assess during (A) the spring peak and (B) the remainder of the stranding period. From left to right, panels give results for code 1, code 2 and code 3 strandings, respectively. Code 1 strandings were only reported during the spring peak period. Note that the scales for codes 2 and 3s have been standardized across time periods..... 109
7. Results from Monte Carlo analysis depicting the probability density function that the model predicted overlap is better ($p < 0.05$) at predicting overlap with vessel activity than Monte Carlo randomly distribution null models. Colored lines represent p-values for condition code 1 (blue), 2 (green), and 3 (red). The black solid line represents a significance value of 0.05 110
8. Relative particle density (%) for probability of point of origin for turtle mortality leading to a stranding classified as condition code 2 with no

apparent injuries during the spring peak. Results include (A) 0%, (B) 2%, and (C) 4% of direct wind forcing on carcass drift, as well as (D) the mean of the results with the varying wind forcing values combined. Note that the color scales have been standardized..... 111

9. Harvest (hundreds of thousands of pounds) by (A) drift gillnets, (B) sink/anchor gillnets, (C) haul seines, (D) whelk pots and traps and (E) crab pots and traps gear. Data was obtained from the Virginia Marine Resource Commission and aggregated over 2009-2014..... 112

10. (A) Menhaden purse seine sets locations (red) aggregated over 2011-2013, obtained from the 2015 Atlantic Menhaden Stock Assessment Report.. Length (km) of net per 5 km by 5 km grid cell for (B) staked gill nets and (C) pound nets based on point locations obtained from the Virginia Marine Resource Commission website for 2017, the current license year at the time of the study..... 113

ABSTRACT

Hundreds of stranded turtles wash up deceased on Virginia's coastline each year, yet the causes of most stranding events are poorly understood. In this thesis, a carcass drift model was developed for the Chesapeake Bay, Virginia, to predict likely locations of mortality from coastal sea turtle stranding records. First, field studies were carried out to better parameterize the drift characteristics of buoyant sea turtle carcasses, namely, probable oceanic drift times and the impact of direct wind forcing on carcass drift. Based on the duration that tethered, free-floating turtle carcasses 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 real turtle carcasses. 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.

The information obtained from these field studies were used to parameterize the oceanographic carcass drift model, which was applied to reported strandings during 2009-2014. Predicted origin of stranding records with probable cause of death identified as vessel strike were compared to commercial boating data. Locations of potential hazardous turtle-vessel interactions were identified in high traffic areas of the southeastern Chesapeake Bay and James River. Commercial fishing activity of various gear types with known sea turtle interactions were compared in space to predicted mortality locations for stranded turtles classified with no apparent injuries, suggesting possible fisheries-induced mortality. Probable mortality locations for these strandings were found to vary between spring peak and summer off-peak stranding periods, but two distinct hotspots were identified in the southwest and southeast portions of the lower bay. Spatial overlap was noted between potential mortality locations and gillnet, seine, pot, and pound net fisheries. These predictions provide clear space-time locations for focusing future research and prioritizing conservation efforts. Nevertheless, the lack of fine temporal and spatial resolution fishing data limited our ability to quantitatively assess most likely causes for specific stranding events. This study both highlights the importance of addressing these data gaps and provides a meaningful conservation and management tool that can be applied to stranding data of sea turtles and other marine megafauna around the globe.

**Integrating Empirical Data and Ocean Drift Models to Better Understand Sea Turtle
Strandings in Virginia**

INTRODUCTION

Sea turtles are highly migratory and long-lived marine species found around the globe. Populations are globally threatened by a large number of processes, such as fisheries bycatch (Lewison et al. 2004b, Finkbeiner et al. 2011), habitat destruction (Dutton and Squires 2008, National Marine Fisheries Service 2013) and climate change (Pike 2014, Katselidis et al. 2014). Anthropogenic interactions are among the most detrimental sources contributing to population decline of all six sea turtle species found in coastal waters of the U.S.: loggerheads (*Caretta caretta*), Kemp's ridleys (*Lepidochelys kempii*), greens (*Chelonia mydas*), leatherbacks (*Dermochelys coriacea*), hawksbill (*Eretmochelys imbricata*), and Olive's ridleys (*Lepidochelys olivacea*) (National Research Council 2010). With all U.S. species listed as endangered or threatened under the U.S. Endangered Species Act (National Research Council 2010) and six of the seven extant sea turtle species found around the world listed on the IUCN Red list of Threatened Species (IUCN 2017), a better understanding of threats that risk population extinction is crucial to the conservation of marine turtles.

Loggerheads are the most common sea turtle species within the U.S. and in Virginia (Keinath et al. 1987, Musick and Limpus 1997). Nesting is primarily concentrated on beaches along the western rim of the Atlantic and Indian oceans, with the majority of United States nesting occurring along the coast from Florida through Virginia. After emerging as hatchlings, turtles migrate to the oceanic zone where they forage and grow until developing into large juveniles. Upon reaching a size of ~40.0-60.0 cm straight carapace length (SCL; ~7-12 years of age), large juvenile turtles recruit back to neritic waters to feed on benthic organisms, exploiting productive nearshore estuarine

systems such as the Chesapeake Bay (Musick and Limpus 1997, Bjorndal et al. 2000, 2001, Snover et al. 2010, Mansfield and Putman 2013). Typically, demersal juveniles will exhibit seasonal migrations between summer temperate foraging zones and offshore wintering grounds south of Cape Hatteras, North Carolina (Musick and Limpus 1997). However, recent studies have noted plasticity in these ontogenetic shifts, with some larger neritic juveniles observed to head back offshore for several years (McClellan and Read 2007, Mansfield et al. 2009). At ~92 cm SCL (~22-26 years of age), loggerheads reach sexual maturity and migrate to adult foraging and nesting habitats (Klinger and Musick 1995, Musick and Limpus 1997, Turtle Expert Working Group 2000).

The Chesapeake Bay and its surrounding coastal waters are critical foraging and developmental habitats for sea turtles (Musick and Limpus 1997, Mansfield et al. 2009), with approximately 5,000 to 20,000 sea turtles (primarily juveniles) inhabiting Virginia's waters each summer (Mansfield 2006, Barco et al. 2014). Turtles enter the bay during the late spring (April-June) when sea temperatures rise above approximately 18-20°C, foraging along the bottom until temperatures fall around September and October (Musick and Limpus 1997, Lutz et al. 2002, Mansfield et al. 2009). They feed primarily on benthic prey, including horseshoe crabs (*Limulus polyphemus*) and blue crabs (*Callinectes sapidus*), and display site fidelity to specific foraging sites both within and between foraging seasons (Mansfield 2006, Seney and Musick 2007). The loggerhead is the most commonly reported sea turtle species found within Virginia's waters, followed by Kemp's ridleys. Loggerheads tend to stay primarily along channel edges and at river mouths, while Kemp's ridleys are typically found in shallower waters, including seagrass beds (Keinath et al. 1987, Byles 1988). Greens and leatherbacks are only occasionally

found in the Bay, and there have only been two hawksbill sea turtles documented in Virginia's waters since 1979 (Mansfield 2006, Barco and Swingle 2014). The IUCN Redlist lists loggerheads as vulnerable, while Kemp's ridleys are classified as critically endangered and are the most seriously endangered sea turtle species worldwide (Turtle Expert Working Group 1998, IUCN 2017). Given the essential role that the Chesapeake Bay plays in the life-cycle of these threatened and endangered sea turtles, strong local management is needed to ensure the maintenance and recovery of these populations.

Hundreds of sea turtles are found stranded on Virginia beaches each year, of which the vast majority wash up deceased (Mansfield 2006, Swingle et al. 2016). The annual number of stranding events in Virginia has fluctuated over the last two decades, ranging from a record high of 531 events in 2003 to a low of 172 in 2011. Within the last decade, approximately 100-300 strandings has been documented per year (Swingle et al. 2016). The majority of strandings occur in late spring when turtles first enter the bay, with remaining events occurring throughout the rest of the foraging season (Mansfield 2006, Swingle et al. 2016). Most of these stranded turtles are in a moderate to severe state of decomposition, severely limiting any information on cause of mortality that can be obtained from the carcass itself (Lutcavage and Musick 1985). The vast majority of stranded loggerheads are juveniles ranging 50-89 cm SCL and are estimated at 15-18 years of age, while stranded juvenile Kemp's ridleys are typically <50 cm SCL and less than 6 years old (Barco and Swingle 2014). As most fatalities likely go unobserved due to low likelihood of landfall and carcass decomposition, these stranding events provide one of the few sources of information on sea turtle mortality (Murphy and Hopkins-Murphy 1989, Epperly et al. 1996). Studies on landfall probability of dead sea turtles in oceanic

locations within the Mid-Atlantic suggest strandings typically do not exceed 10-20% of total death (Epperly et al. 1996, Hart et al. 2006). Although the oceanic sites of these studies likely exhibit greater offshore movement than the nearshore, estuarine environmental of the Chesapeake Bay, extrapolating the conservative estimate of strandings representing 20% of total mortality to data in this region suggests that a minimum of 500-1500 turtle deaths occur per year in Virginia. Conservation and recovery goals should be focused on understanding and reducing mortality events (Crouse et al. 1987), yet relatively little is known about the causes of stranding events in the region (Mansfield 2006). Importantly, Virginia's waters host loggerheads from several different western Atlantic subpopulations (Conant et al. 2009, Mansfield et al. 2009), and thus local mortality can lead to detrimental impacts among multiple loggerhead subpopulations (Mansfield et al. 2009).

Given the protected status of sea turtles, the potentially highly detrimental effects of juvenile sea turtle mortality for population persistence (Crouse et al. 1987) and the importance of the Chesapeake Bay for multiple different sea turtle populations (Conant et al. 2009, Mansfield et al. 2009), these strandings have long been a concern for management. A number of management actions, including gear modifications for Virginia pound net fisheries, have been implemented over the last 15 years to reduce anthropogenic sea turtle mortality in the bay (National Marine Fisheries Service 2006, 2015). Nevertheless, strandings continue to occur and the causes of most mortality events remain unclear due to lack of physical signs of the cause of mortality and/or the state of carcass decomposition (Lutcavage and Musick 1985). Identified probable causes of sea turtle mortality in Virginia's waters include poor health, cold stunning, boat strikes and

interactions with fishing gear. The Chesapeake Bay and Virginia's coastal waters are subject to heavy commercial and recreational public use (Terwilliger and Musick 1995), and thus sea turtles in this region have a high probability of interaction with human activities. Furthermore, as temperatures increase due to climate change, the Chesapeake Bay is predicted to become much more favorable to sea turtles (Pike 2014), and, therefore, it is extremely important to identify and manage for any anthropogenic causes of mortality now before there has been a significant increase in turtle usage of the bay. More precise identification of likely locations of mortality events based on analyses of surface transport patterns is essential to reducing negative human-turtle interactions and ensuring the long-term sustainability of sea turtle populations.

The Virginia Aquarium & Marine Science Center Stranding Response Program (VAQS) has been responding to sea turtle strandings in Virginia since 1987, yet much remains to be learned from this extensive dataset regarding the causes of turtle stranding events (Swingle et al. 2016). Research is needed to identify at-sea mortality locations in order to find potential causal mechanisms for mortality and provide focus areas for conservation. After sea turtles die, their bodies bloat and float to the surface (if not entangled), where they may be transported by winds and currents to the coast. Observations of these stranding events provide a general time period and region for mortality events, but careful interpretation in light of prevailing surface transport conditions, carcass decay processes and potential threats to sea turtle survival is needed to identify probable space-time coordinates of mortality events and associate these with causal mechanisms. By decreasing the knowledge gap surrounding these annual stranding

events, this study will enhance the conservation and recovery of sea turtle populations that inhabit the Chesapeake Bay and Virginia coastal waters.

In this thesis, ocean transport studies were used to infer likely turtle mortality locations from data on stranding locations. The ultimate objectives are to identify causal mechanisms for sea turtle mortality in the bay and use this information to develop targeted management actions aimed at reducing mortality rates. This thesis details two main components to achieve these goals. Chapter 1 highlights field experimentation conducted to better parameterize sea turtle carcass drift, namely (1) the probable time turtles spend drifting in the bay prior to beaching at stranding locations and (2) the amount of direct wind forcing needed to properly estimate drift of a sea turtle carcass. These empirically-obtained parameters are directly fed into the development of an oceanographic drift model used to predict likely locations of at-sea mortality for geographic areas where large numbers of deceased turtles beach. Chapter 2 contains oceanographic simulations of carcass drift trajectories to observed stranding times and locations for specific stranding events. Probable mortality locations within the bay are identified and analyzed for links to potential anthropogenic causes. The spatio-temporal information derived from this study will be invaluable in identifying focal areas for sea turtle conservation in Virginia's waters, highlighting specific geographic areas for management efforts to concentrate on alleviating threats.

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CHAPTER 1:

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

ABSTRACT

Sea turtle strandings provide important mortality information, yet knowledge of turtle carcass at-sea drift and decomposition characteristics is 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 real turtle carcasses. 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. A Chesapeake Bay oceanographic drift model was developed 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 indicate that sea turtle drift time may be quite short and that direct wind forcing is important for drift trajectories. Knowledge of these parameters will improve our ability to interpret stranding events around the globe.

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 gasses 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 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 its 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.

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.

Decomposition study

When stranded turtles are found on the beach (which generally occurs soon after stranding in populated areas), carcass condition is assessed on a condition code scale from 1 (freshly deceased; as discussed above, 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' 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 four-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 no obvious, large differences in decomposition between individuals of different sizes or species were observed.

Drift study

To assess the effect of wind forcing on turtle drift, three types of drifters were used: actual turtle carcasses, bucket drifters and wood-Styrofoam 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). A satellite-transmitting GPS receiver (Assetlink TrackPack transmitters) was mounted on a self-righting crab pot buoy that was attached to the turtle through its carapace (Figure A3). The carcasses were frozen and stored prior to use.

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-Styrofoam turtle drifters were constructed out of layers of wood and Styrofoam 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 carcasses. Both bucket drifters and wood-Styrofoam 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 wooden 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 and redeployed for subsequent deployments. 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 57feet 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-Styrofoam turtles and true turtle 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-Styrofoam 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.

Drifter data used in leeway analyses were limited to the first 2.5-8.5 hours after release due to the separation of drifters over time. Drifter 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). 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 carcasses and wood-Styrofoam turtles included categorical variables for each deployment, (i.e. drifter release trial), turtle carcass or wood-Styrofoam turtle, and the bucket being compared with a given turtle or wood-Styrofoam turtle trajectory. When estimating wood-Styrofoam turtle leeway, both bucket and wood-Styrofoam turtle were considered random nested effects inside wind speed and deployment. When estimating turtle carcass leeway, bucket was a random effect nested inside wind speed, deployment and turtle carcass. 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 turtle carcass.

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 or wood-Styrofoam turtle 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.

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 Chesapeake Bay, 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.

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) for 2001-2005, 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). Computer simulations were configured to release 1,000 particles randomly throughout the bay every 6-hours with particle tracking time 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 the 2016 time period at the time of the study, 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. 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 25-km² grid.

RESULTS

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). 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°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°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.

Drift study

Wind speed, deployment and individual turtle carcass 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 carcasses 1 and 2, turtle carcass 3 during deployment 3, and wood-Styrofoam turtles during deployments 1 and 3-4. Cross-wind leeway was not found to be significant for any turtle carcass, but was significant for most of the wood-Styrofoam turtle 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 carcasses and wood-Styrofoam turtles, 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 carcasses and wood-Styrofoam turtles 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.

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°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).

DISCUSSION

Our study provide the first use of controlled 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. In addition, this research is also among the first efforts to use

oceanographic modeling to identify potential areas of turtle mortality in Virginia's waters.

Decomposition study

The post-mortem interval is a key element in forensic investigations. This study provides one of the first data sets detailing decomposition rates of sea turtles in controlled field experiments, providing a better estimation of the postmortem interval of stranded turtles based on reported condition code.

All eight turtle carcasses in this study decomposed to bones in less than 18 days, in water temperatures averaging 17-29°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°C) to 2-days in cooler waters (17.5-20.5°C). It is worthwhile to note that the carcasses in this study were frozen

prior to use, and previously frozen-thawed animals have been shown to decompose on the order of hours to days faster than non-frozen animals, although the sequence of decomposition remains the same (Micozzi 1986). Thus, 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°C waters, and after 4-5 days in 14-22°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° 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.

Drift study

Our leeway drift estimates of sea turtle carcasses are one of the first attempts to parameterize the drift characteristics of deceased sea turtles prior to stranding. 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. 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. Along-wind leeway for wood-Styrofoam turtles was

similar in magnitude to that of turtle carcasses, 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 and wood-Styrofoam turtle leeway coefficients, suggestive of environmental differences between deployments being a source of leeway variability (because the same wood-Styrofoam turtles 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 (Carcass 2), which was used exclusively in the first deployment, was 3.59%, whereas for the smallest turtle carcass (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. 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).

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.

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.

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. 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.

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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-Styrofoam turtle	CCL: 88.5 SCL: 73.6
Turtle Carcass 1	CCL: 83.5* SCL: 76.7*
Turtle Carcass 2	CCL: 101.3* SCL: 93.5
Turtle Carcass 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-Styrofoam turtles	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
	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 No.							
	1	2	3	4	5	6	7	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 ^b	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*

b. Measured notch to tip

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 carcasses and wooden-Styrofoam turtles 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							
Drift object	Deploy.	Unconstrained				Constrained	
		Y-int.	Slope (%)	95% C.I. (%)	Signif.	Slope (%)	95% C.I. (%)
Turtle carcass 1	1	-5.45	2.26	1.08-3.44	***	2.15	1.78-2.52
Turtle carcass 2	1	15.72	3.26	0.85-5.67	**	3.59	2.84-4.35
Turtle carcass 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
Wooden-Styrofoam turtles	1			2.19-6.35		3.54	2.19-6.35
		-34.9	4.27		***		
	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							
Drift object	Deploy.	Unconstrained				Constrained	
		Y-int.	Slope (%)	95% C.I. (%)	Signif.	Slope (%)	95% C.I. (%)
Turtle carcass 1	1	22.53	1.09	(-2.31)-4.49		1.56	0.50-2.63
Turtle carcass 2	1	-48.92	1.34	(-1.54)-4.22		0.31	(-0.60)-1.22
Turtle carcass 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
Wooden-Styrofoam turtles	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							
Drift object	Deploy.	Unconstrained				Constrained	
		Y-int.	Slope (%)	95% C.I. (%)	Signif.	Slope (%)	95% C.I. (%)
Turtle carcass 1	1	14.99	3.45	1.89-5.01	***	3.77	3.28-4.25
Turtle carcass 2	1	138.01	1.53	(-0.24)-3.30	.	4.43	3.76-5.09

Turtle carcass 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
Wooden- Styrofoam turtles	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

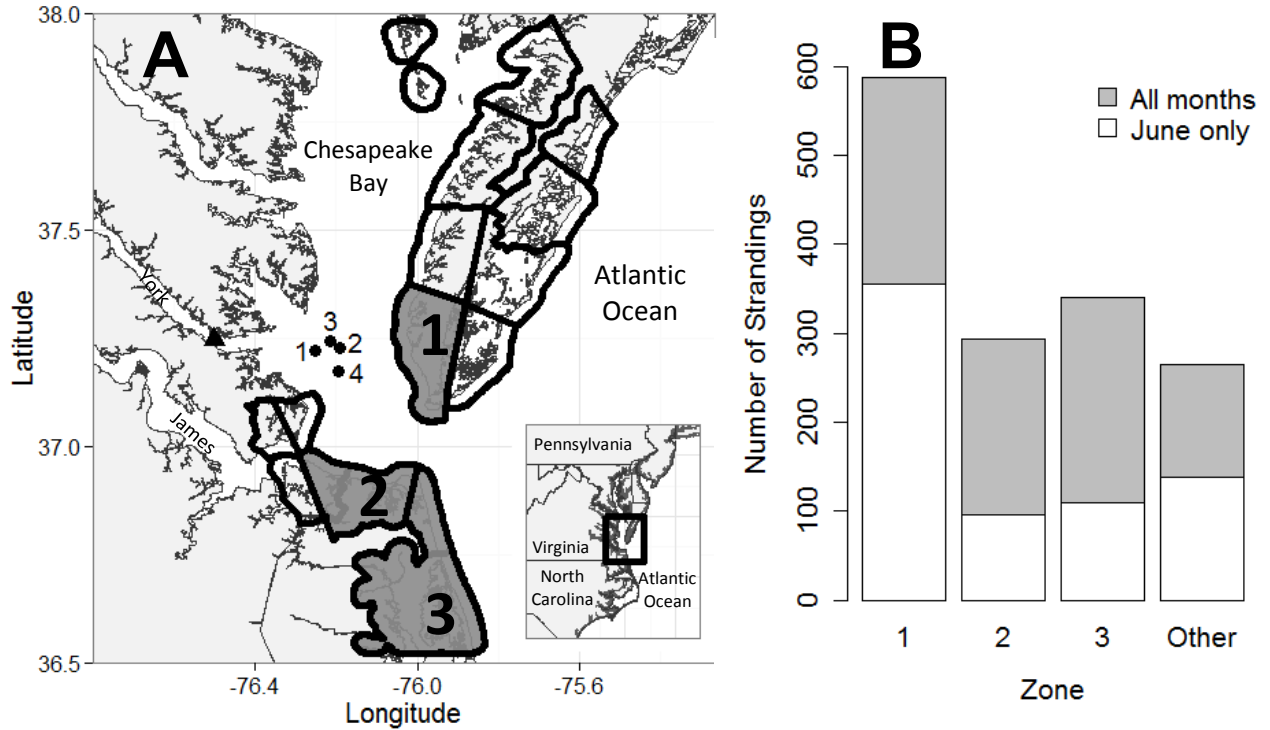


FIGURE 1. (A) Location of study sites within the Chesapeake Bay, VA, including the decomposition rate study (triangle), release points for the four drifter deployments (circles), and target zones for the oceanographic simulations (black outline). The target zones represent county-level areas which make 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.

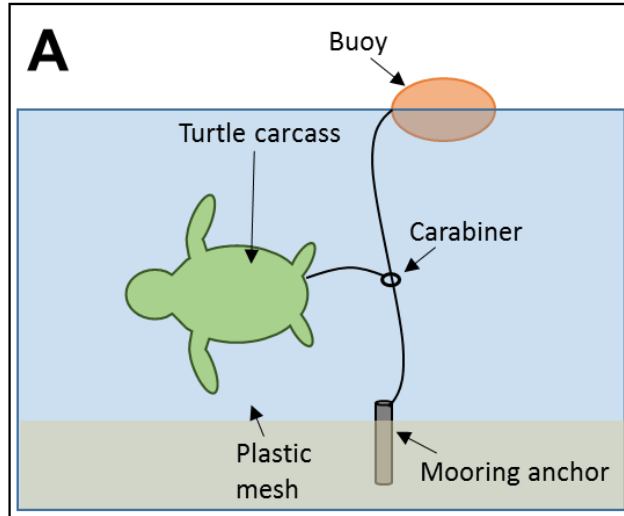


FIGURE 2. (A) Schematic of the decomposition study experimental design. (B) Image of a turtle carcass floating at sea. (C) Image of a turtle carcass on shore.

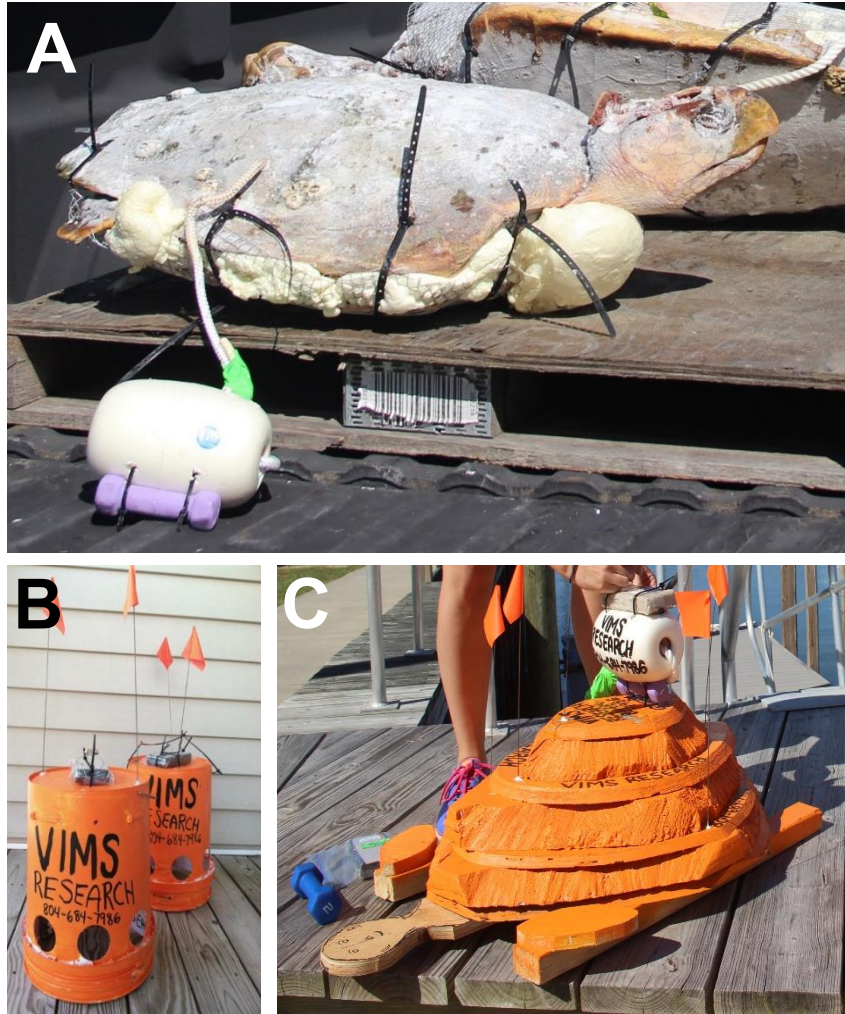


FIGURE 3. (A) Turtle carcass, (B) bucket, and (C) wood-Styrofoam drifters.

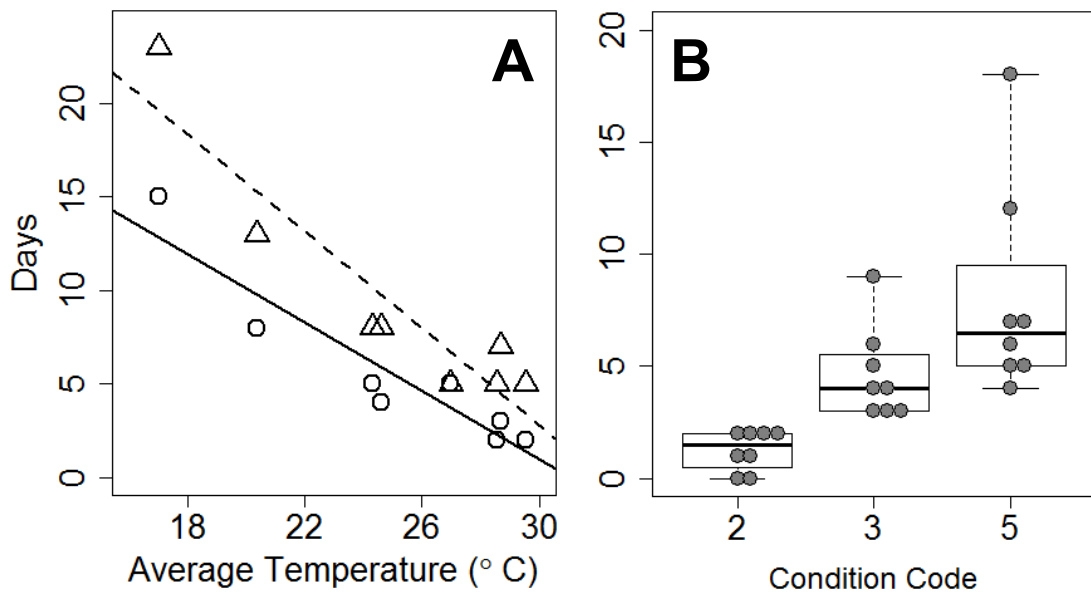


FIGURE 4. (A) Duration of positive buoyancy (circles, solid line) and time to total decay (triangles, dotted line) vs average water temperature ($^{\circ}\text{C}$). (B) Boxplot of the minimum number of days to reach each condition code stage.

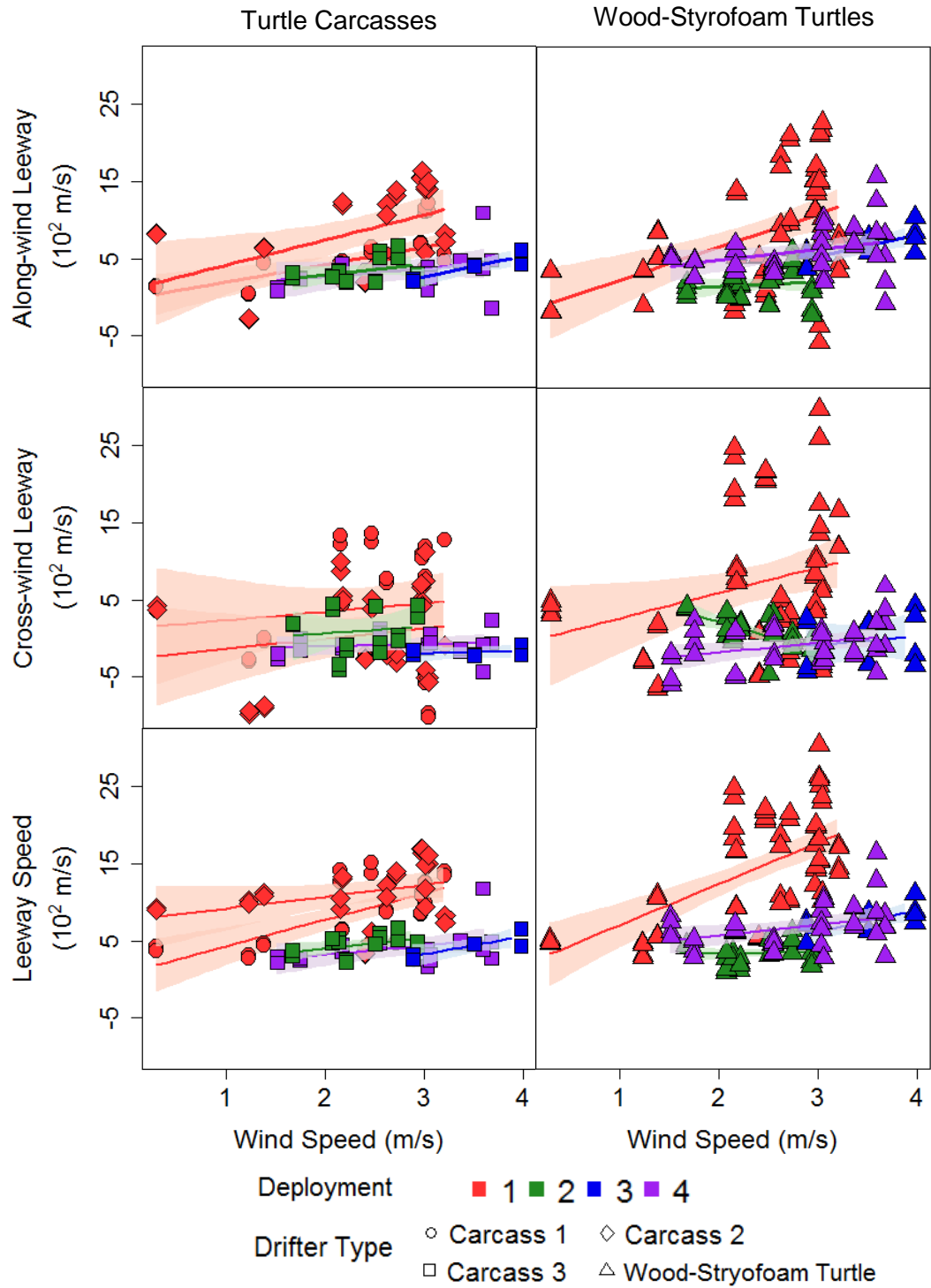


FIGURE 5. (A) Along-wind component of leeway (m/s), (B) Cross-wind component of leeway (m/s), and (C) Leeway speed vs. wind speed (m/s) for each turtle carcass-deployment combination. Values are averaged over half hour periods. Solid lines represent the unconstrained linear regression mean and the shaded polygon represents the 95% confidence intervals.

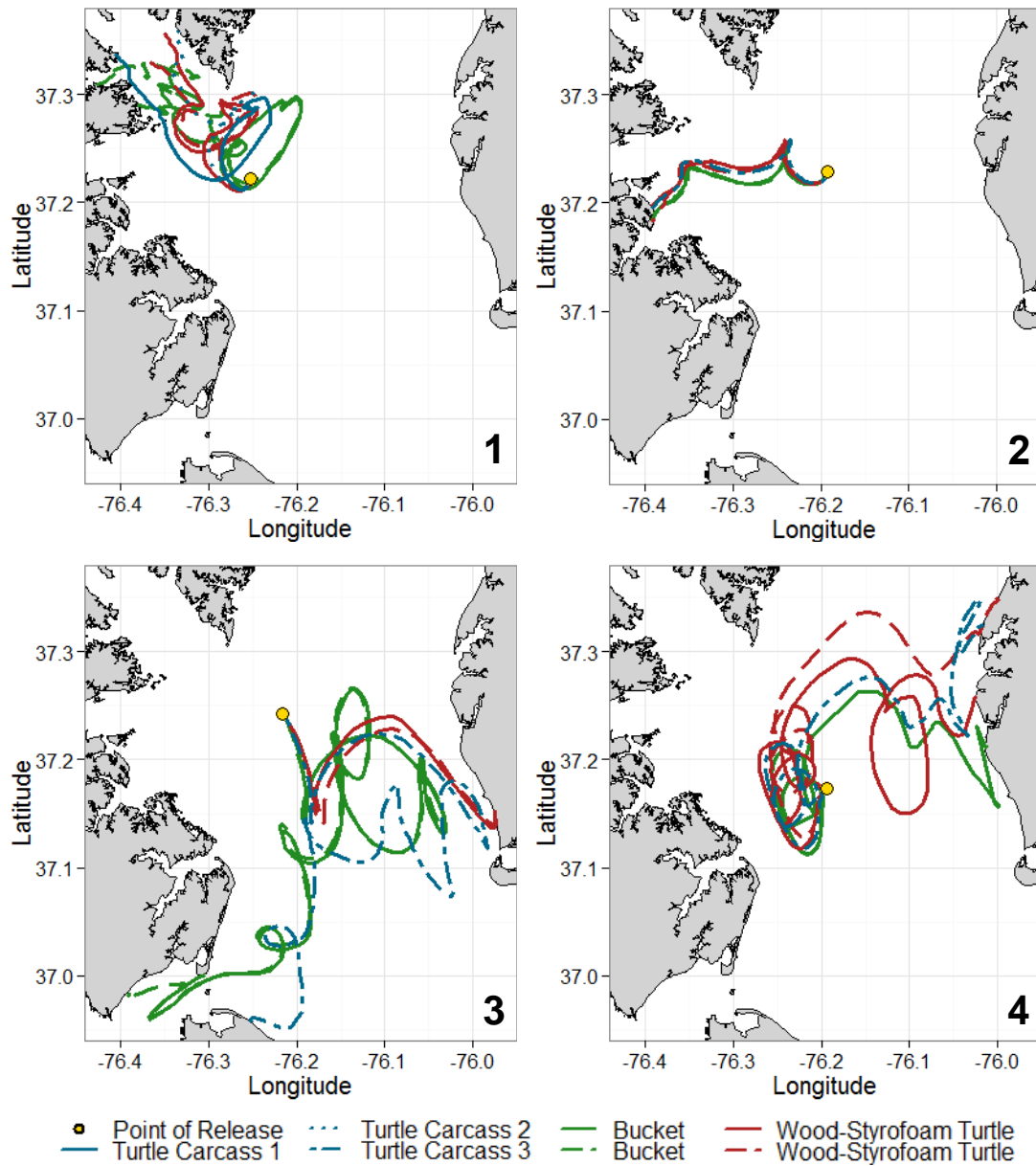


FIGURE 6. Complete drift tracks of all individual drifters during the four deployments.

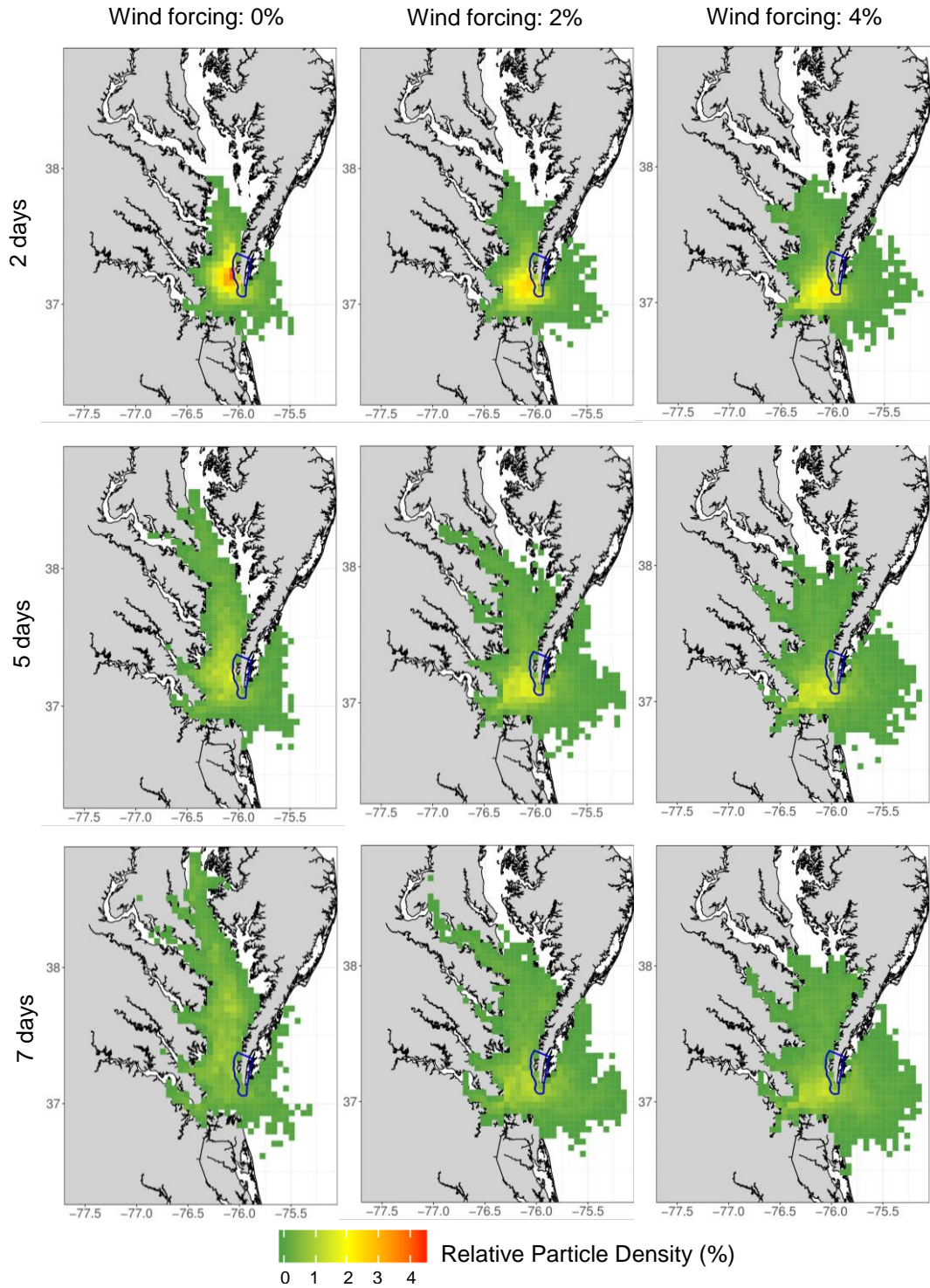


FIGURE 7. Relative particle density (%) for probability of point of origin 2, 5 and 8 days prior to stranding in Zone 1, as outlined in blue. Results include 0%, 2% and 4% of direct wind forcing on carcass drift. Simulation results are a composite over 5 months of June for the years 2001-2005.

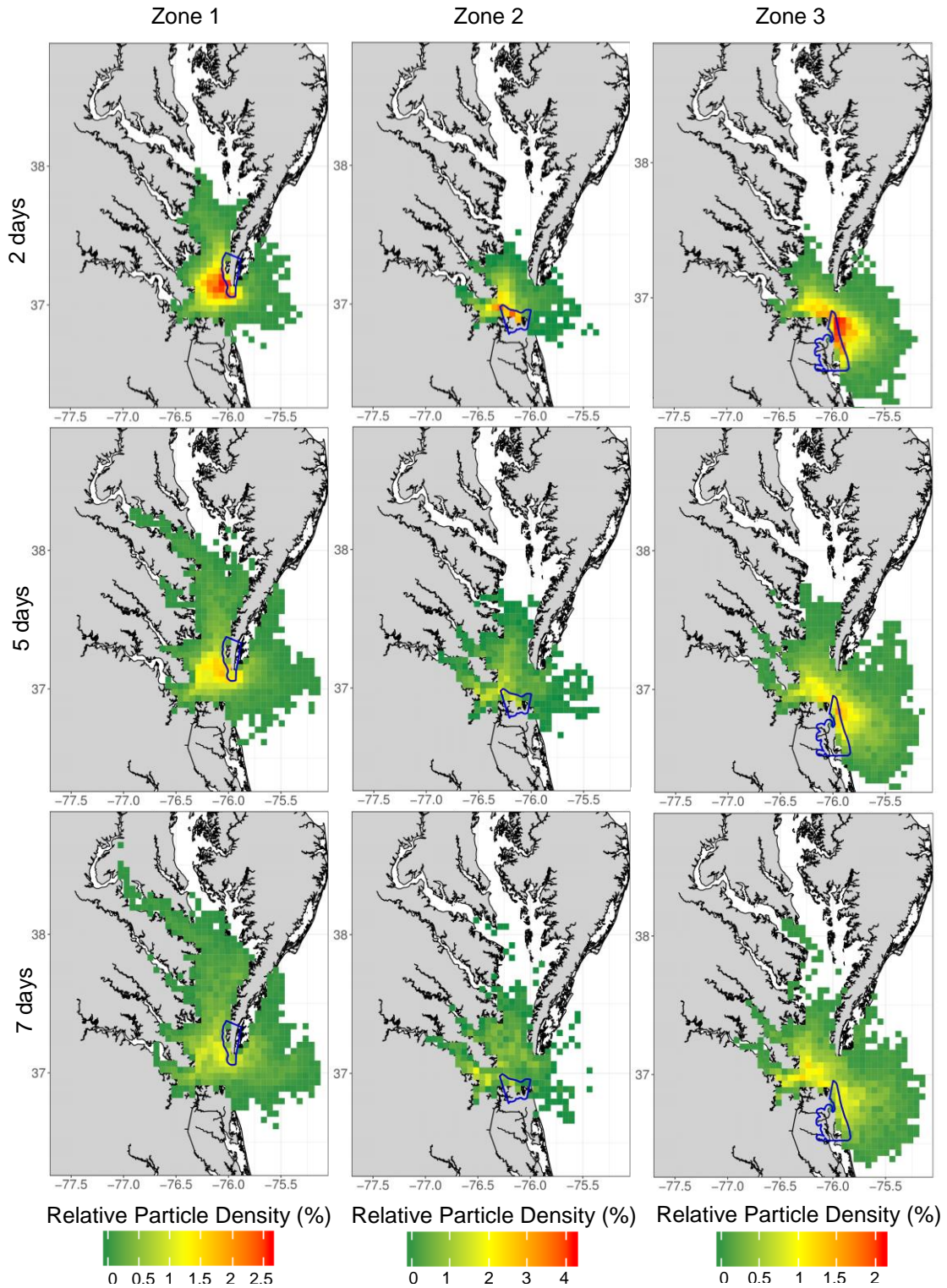


FIGURE 8. Relative particle density (%) for probability of point of origin 2, 5 and 8 days prior to stranding in outlined zone with 2% of direct wind forcing on carcass drift. Simulation results are a composite over 5 months of June for the years 2001-2005.

Code 1
Fresh dead

Code 2
Moderately
decomposed

Code 3
Severely
decomposed

Code 5
Bones only



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

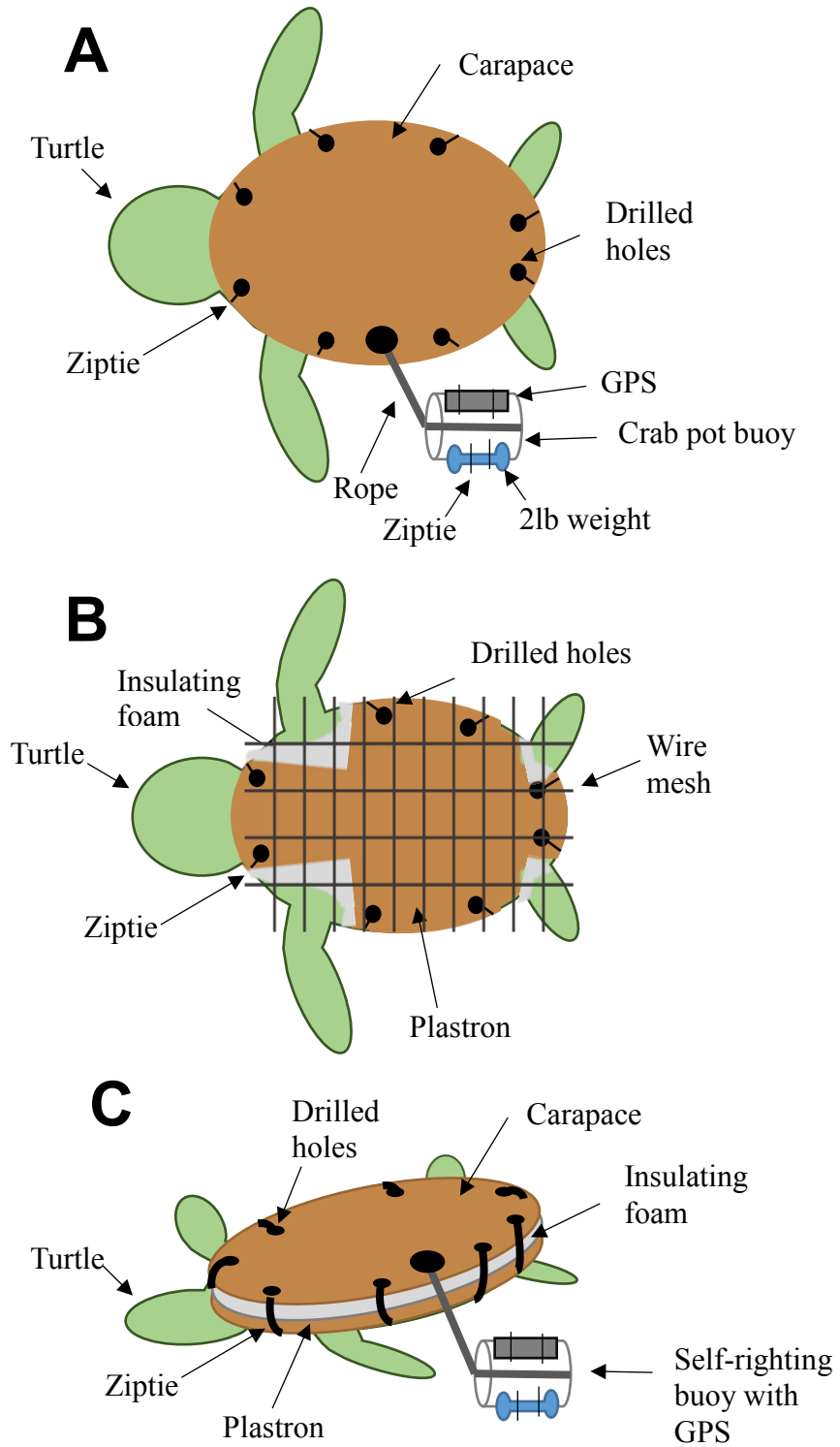
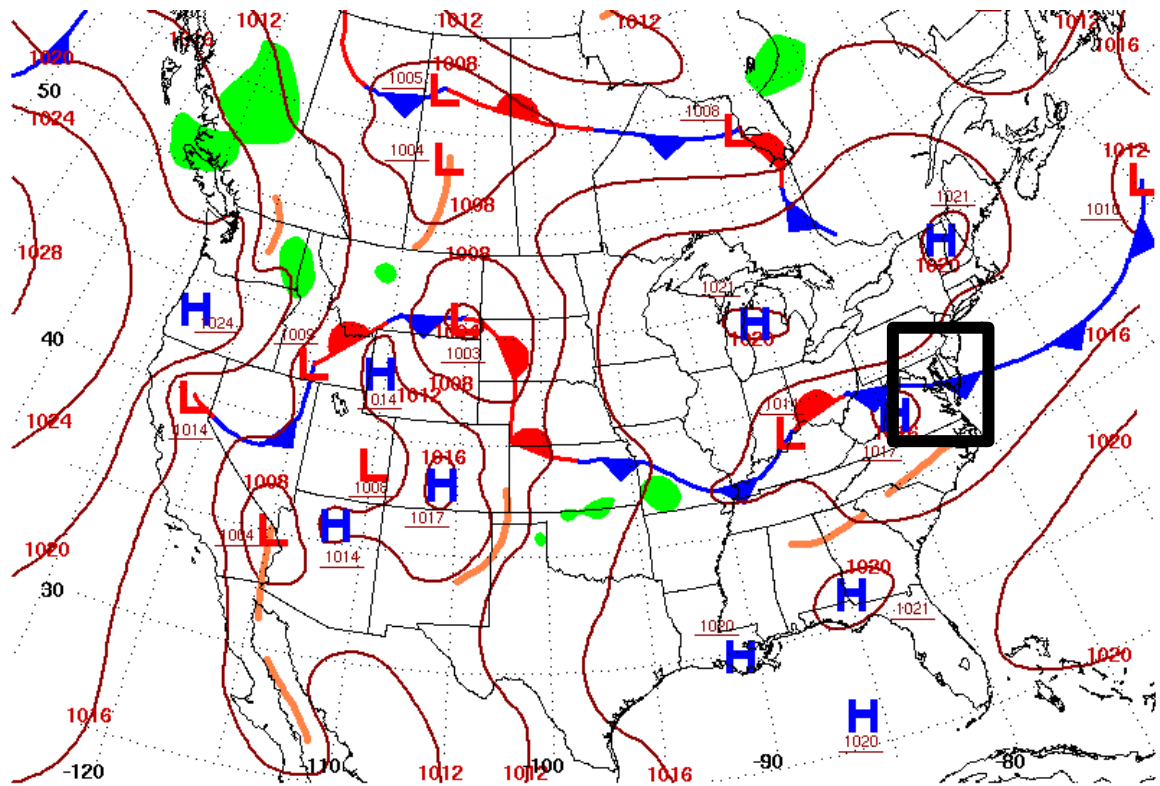


FIGURE A2. Schematic of sea turtle carcass drifter, including (A) carapace view, (B) plastron view, and (C) side-profile.



FIGURE A3. Self-righting buoy attachment with GPS for wood-Styrofoam and turtle carcass drifters.



Surface Weather Map at 7:00 A.M. E.S.T.

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.

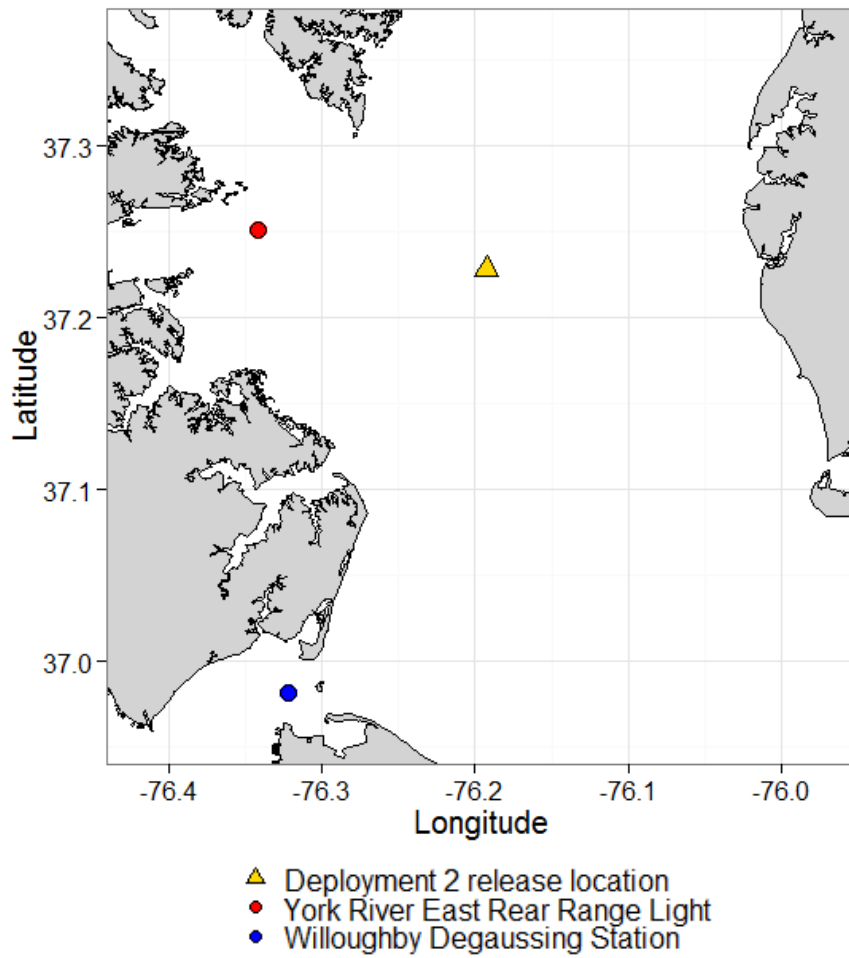


FIGURE A5. Locations of monitoring stations 8637611 York River East Rear Range Light (red circle), 8638614 Willoughby Degaussing Station (blue circle), and deployment 2 release location (yellow triangle).

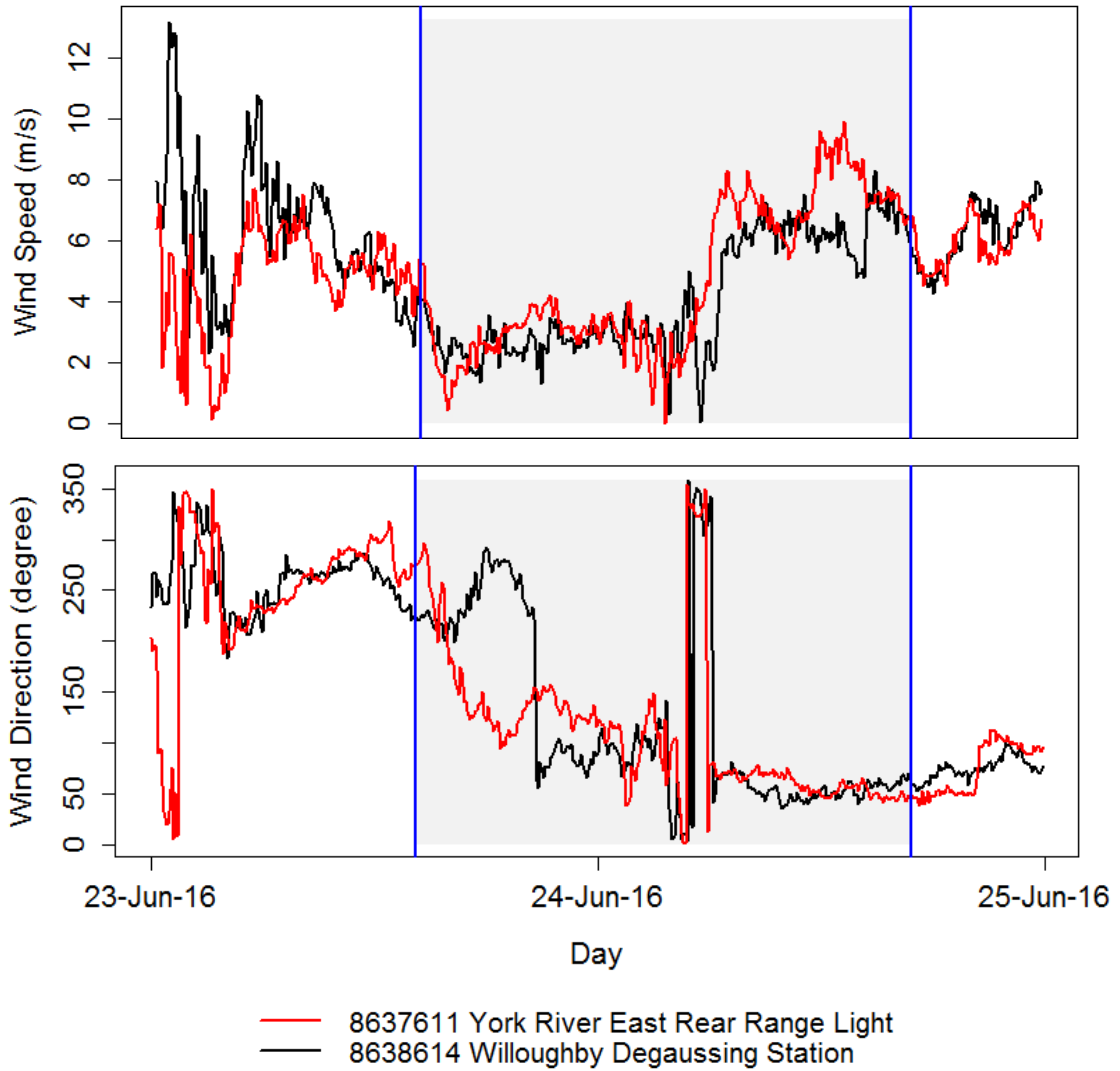


FIGURE A6. Reported wind speed (m/s) and wind direction (degrees from true north) from monitoring stations 8637611 York River East Rear Range Light and 8638614 Willoughby Degaussing Station. Shaded area represents the full time period of deployment 2.

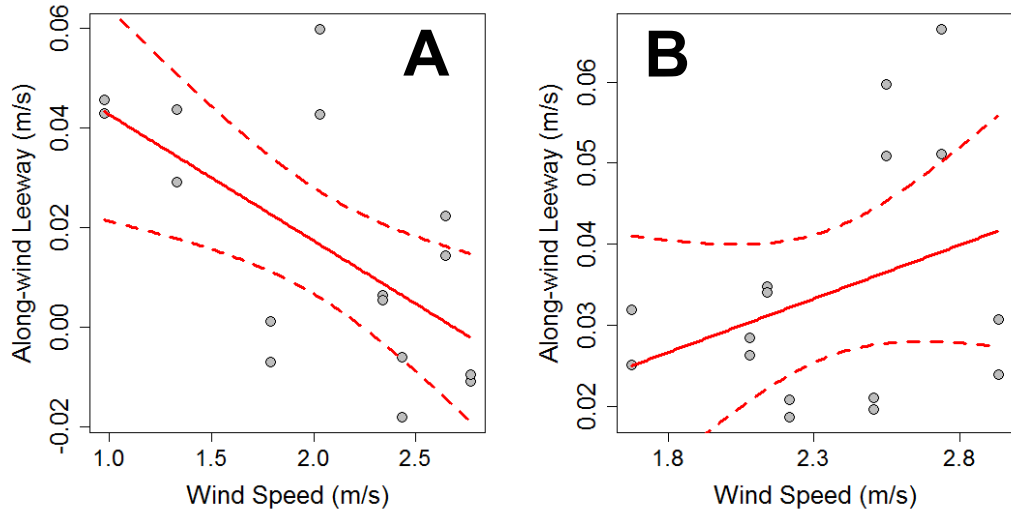


FIGURE A7. Deployment 2 results of the along-wind component of leeway for turtle carcass 3 using metrological data from monitoring stations (A) 8637611 York River East Rear Range Light and (B) 8638614 Willoughby Degaussing Station. Dashed lines represent 95% confidence intervals.

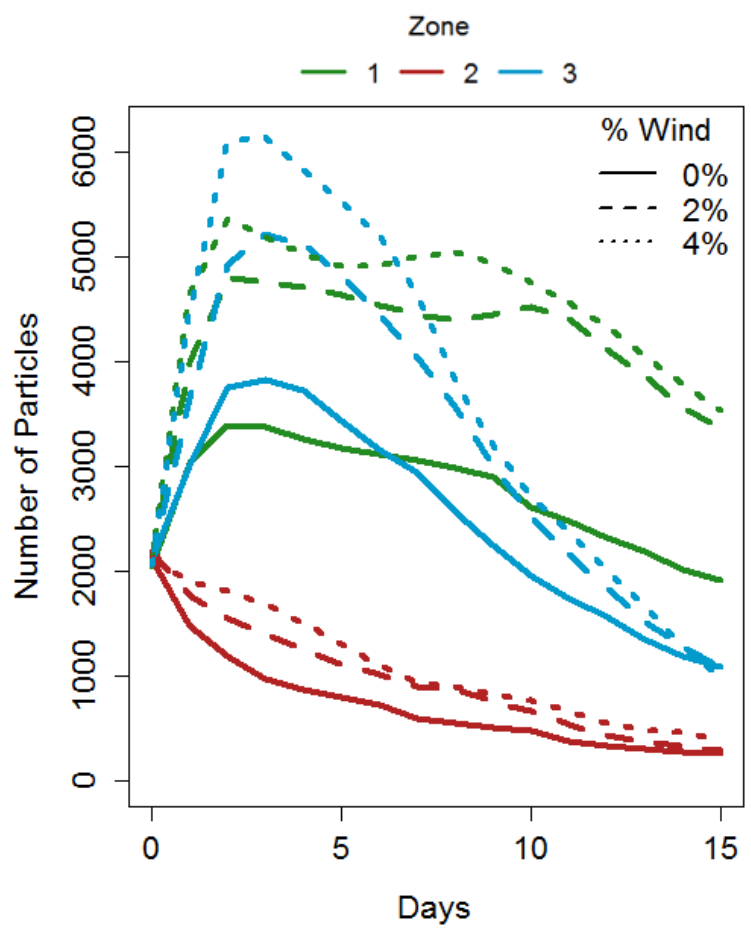


FIGURE A8. Relative number of particles from the oceanographic model making landfall over elapsed time (days). Simulation results are a composite over 5 months of June from the years 2001-2005.

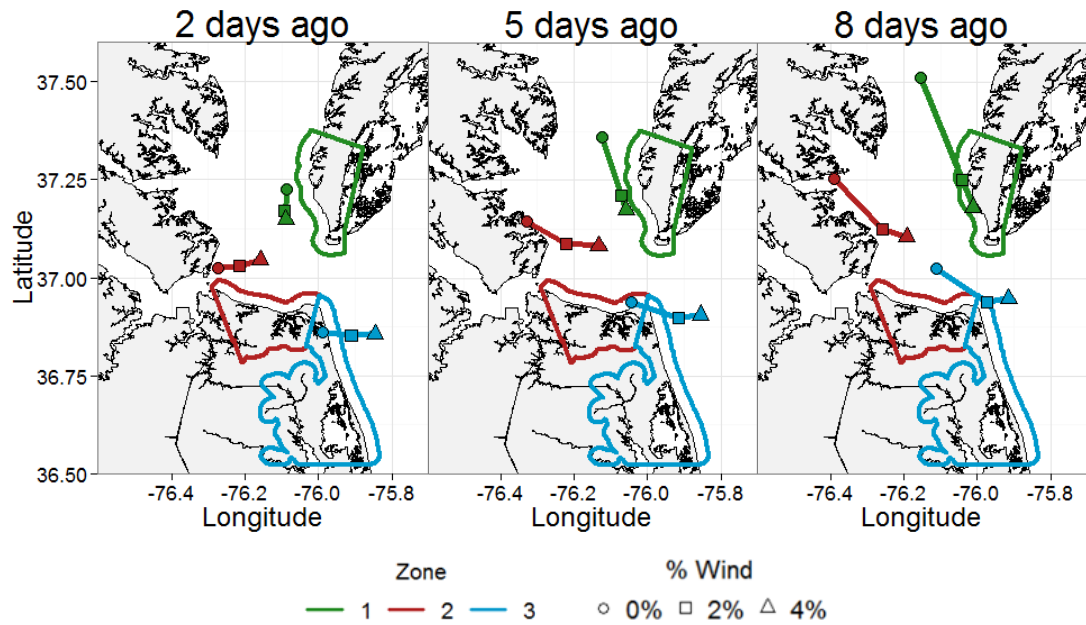


FIGURE A9. Mean starting locations 2, 5, and 8 days prior to stranding in top zones. Simulation results are a composite over 5 months of June from the years 2001-2005.

CHAPTER 2:

Probable locations of sea turtle mortality from strandings using experimentally-calibrated, time- and space-specific carcass drift models

ABSTRACT

Sea turtle stranding events provide a unique opportunity to study drivers of mortality in marine megafauna, but causes of strandings are generally poorly understood. We developed a carcass drift model for the Chesapeake Bay, Virginia, USA, to predict likely locations of mortality from coastal sea turtle stranding records during 2009-2014. Key model advancements include realistic direct wind forcing on carcasses, temperature driven carcass decomposition and the targeting of specific stranding events to develop mortality location predictions for individual strandings. Predicted origin of vessel strike stranding records were compared to commercial boating data, and hotspots of potential hazardous turtle-vessel interactions were identified in high traffic areas of the southeastern Chesapeake Bay and James River. Commercial fishing activity of various gear types with known sea turtle interactions were compared in space to predicted mortality locations for stranded turtles classified with no apparent injuries, suggesting possible fisheries-induced mortality. Probable mortality locations for these strandings were found to vary between spring peak and summer off-peak stranding periods, but two distinct areas were identified in the southwest and southeast portions of the lower bay. Spatial overlap was noted between potential mortality locations and gillnet, seine, pot, and pound net fisheries. These predictions provide clear space-time locations for focusing future research and prioritizing conservation efforts. Nevertheless, the lack of fine temporal and spatial resolution fishing data limited our ability to quantitatively assess most likely causes for specific stranding events. This study both highlights the importance of addressing these data gaps and provides a meaningful conservation and management tool that can be applied to stranding data of sea turtles and other charismatic marine fauna around the globe.

INTRODUCTION

Many of the world's charismatic marine megafauna are highly threatened by a mixture of anthropogenic pressures (Lewison et al. 2004a, Read et al. 2006, Crain et al. 2009) and global climate change (Learmonth et al. 2006, Poloczanska et al. 2009). Among these emblematic species are marine sea turtles, of which six out of the seven species worldwide are listed on the IUCN Red List of Threatened Species (<http://www.redlist.org>). For sea turtles and other marine megafauna, a better understanding of the impacts of anthropogenic activities on these species is essential to assessing risk of population extinction and identifying effective conservation strategies. Although sea turtle strandings provide an important opportunity to study turtle mortality and mitigate against it, the causes of strandings are generally poorly understood. Identifying potential causes of mortality of stranded sea turtles can be extremely challenging due to state of carcass decomposition and the lack of physical evidence of the cause of mortality (Hart et al. 2006, Koch et al. 2013). In particular, interactions with fishing gear often do not leave marks on turtles, thus using injuries noted at time of stranding to attribute cause of death has been suggested to grossly underestimate fisheries-induced mortality (Barco et al. 2016). Fishing activity has been noted as a driver of turtle mortality worldwide, with lethal sea turtle interactions documented in gear types including longlines, trawls, gillnets, pound nets, dredges, seines and pots (Lewison et al. 2004a, Zollett 2009, Wallace et al. 2010, Finkbeiner et al. 2011). Despite the current vulnerability of sea turtle species and known interactions with recreational and commercial fishing gear, as well as boating activity more generally, management actions are still frequently hindered by lack of specific information on where and when negative human-turtle interactions occur.

The Chesapeake Bay and its surrounding coastal waters are critical foraging and developmental habitats for thousands of sea turtles that use these waters seasonally (Musick and Limpus 1997, Mansfield 2006). However, hundreds of deceased turtles are found stranded on Virginia's coastline each year. The Virginia Aquarium & Marine Science Center's Stranding Response Program (VAQS) has been responding to strandings throughout the state since 1987, documenting approximately 100-300 events annually in the past decade (Swingle et al. 2016). Strandings are observed throughout the year, although there is a strong spring peak occurring in May and June when turtles are first entering the bay (Lutcavage and Musick 1985, Coles 1999). Mortality continues at a high level throughout the summer, until turtles migrate out of the Bay in the early fall to avoid cold winter temperatures (Mansfield et al. 2009). Juvenile loggerheads are the most commonly reported sea turtles found within Virginia's waters (Barco and Swingle 2014). Importantly, Virginia's waters provide crucial habitats for loggerheads from several different western Atlantic subpopulations (Conant et al. 2009, Mansfield et al. 2009), thus local mortality can lead to detrimental impacts among multiple loggerhead subpopulations (Mansfield et al. 2009). The second most common species documented in Virginia (Lutcavage and Musick 1985, Coles 1999, Barco and Swingle 2014), Kemp's ridleys are the most endangered sea turtle species around the globe (Turtle Expert Working Group 1998). Strandings likely represent a minimal measure of actual at-sea mortality, with some studies estimating stranding events to represent only 10-20% of total deaths (Epperly et al. 1996, Hart et al. 2006). Given the essential role that the Chesapeake Bay plays in the life-cycle of these sea turtles and the potential for large,

unobserved mortality, detailed information on times, places and causes of mortality are essential to maintaining and increasing these populations.

Relatively little is known about the causes of stranding events in this region (Mansfield 2006). In Virginia, most stranded sea turtles are in a moderate to advanced state of decomposition, making cause of death impossible to assess (Lutcavage and Musick 1985). For those turtles that can be assessed, a large majority either exhibit signs of death by vessel strike or are classified with no apparent injuries. Most dead stranded turtles in both these categories appear to be healthy prior to death, suggesting they were not already compromised in any way prior to mortality (Barco et al. 2016). Although a number of factors may contribute to mortality of Chesapeake Bay turtles (i.e. environmental variables and prey availability), the circumstances surrounding strandings classified with no apparent injuries, including relatively healthy turtles prior to death, a general lack of external wounds, and turtles with finfish in their stomachs, are consistent with fisheries interactions as a likely cause of death. Turtles are believed to not be fast or agile enough to naturally catch and consume fish (Bellmund et al. 1987), with studies suggesting that turtles are only able to prey upon large amounts of finfish through interactions with fishing gears (Bellmund et al. 1987) or bycatch (Robert Shoop and Ruckdeschel 1982). Historic declines of horseshoe crab and blue crab populations in the Bay, the preferred prey items of loggerheads, has correlated with an increase in the presence of fish in the guts of stranded turtles in this region, possibly indicating a higher likelihood of fisheries interaction (Seney and Musick 2007). Turtles in this region have been documented caught or entangled in pound net leader hedging, gillnets, trawl nets, crab pot lines and whelk pot lines (Bellmund et al. 1987, Keinath et al. 1987, Mansfield

et al. 2001). Although there is no concrete evidence of the Chesapeake Bay's menhaden purse seine fishery causing sea turtle mortality, other purse seine fisheries in the region are known to kill turtles (Silva 1996) and there is a question whether the menhaden fishery may be a significant source of turtle mortality. Narrowing down this list of potential drivers for sea turtle mortality in the bay to just the most important causes, locations and time periods is essential to developing targeted conservation strategies for these threatened species.

Observations of stranding events provide a general time period and region for mortality events, but careful interpretation in light of sea turtle carcass drift parameters and potential threats to sea turtle survival is needed to identify probable space-time coordinates of mortality events and associate these with probable causal mechanisms. After sea turtles die, their bodies bloat and float to the surface (if not entangled). Partially submerged and acting as drifting objects, carcasses are transported by winds and currents. Landfall may occur if conditions are favorable to onshore transport and the turtle carcass does not decompose and sink before reaching a coastline. Oceanographic modeling and drift studies have been used in the past to understand mechanisms for larval release and dispersal (Garavelli et al. 2012), as well as to predict trajectories of drifting human bodies (Carniel et al. 2002) and cetacean carcasses (Peltier et al. 2012). A limited number of recent studies have applied this approach to sea turtle carcasses in other geographic regions (Hart et al. 2006, Nero et al. 2013, Koch et al. 2013), providing valuable insight on stranding causes and likelihood.

In this study, we develop an oceanographic drift model for the Chesapeake Bay simulating the drift patterns of dead turtles to stranding locations to identify likely

locations of sea turtle mortality. Results from field experiments were used in the model to parametrize the probable oceanic drift time as a function of temperature and the impact of direct wind forcing on carcass drift (Chapter 1). The model was applied to individual sea turtle stranding observations in coastal areas of Virginia and most probable mortality locations within the region were identified for specific classes of strandings with similar characteristics (e.g., probable cause of death, state of carcass decomposition), providing a basis for quantitative and qualitative comparisons with spatial distributions of potential causes of mortality in the Bay. This research represents the first use of a carcass drift model to identify likely locations of mortality based on stranding records for the Chesapeake Bay, and it includes a number of methodological improvements that can be applied to stranding data for sea turtles and other marine megafauna around the globe.

METHODS

A model simulating the drift of dead sea turtles prior to stranding was developed using the offline Lagrangian drift simulation tool Ichthyop version 3.3. The model was configured to release 20,000 pseudo-particles (i.e. simulated particles) throughout the bay every three hours and run forward in time based on transport estimates from atmospheric and ocean circulation models. Pseudo-particles arriving at stranding locations at the appropriate time (i.e. probable date of landfall based on reported stranding date) and having a desired set of conditions (see below) were identified. The release points for many forward trajectories were aggregated to create a probability distribution representing likely mortality locations of stranding events. Estuarine circulation information was derived from an implementation of the Regional Ocean Modeling System (ChesROMS; version 3.6) for the Chesapeake Bay area (Feng et al. 2015) and

wind forcing was obtained from the North American Regional Reanalysis (NARR) (Mesinger et al. 2006). ChesROMS, NARR and Ichthyop internal timesteps were all 3 hours.

The amount of direct wind forcing on the surface transport of turtle carcasses is estimated to be 1-4% of wind speed (Chapter 1, Nero et al. 2013). Wind forcing was added to the ChesROMS currents at 0%, 2% and 4% of wind speed to assess sensitivity of estimates to wind forcing levels over the range of experimentally-observed levels (Chapter 1). Resulting particle trajectories therefore represent the combined impacts of wind and currents on carcass movements. When presenting model results, 2% wind forcing will be used unless otherwise indicated because it is closest to experimentally observed values.

Stranding data

Sea turtle stranding data collected by VAQS during 2009-2014 were assessed. Strandings can encompass dead and live animals, but the potential for active swimming of sick turtles found alive can complicate the simulation of their movements. In this study, we focus only on deceased individuals found washed ashore and refer to these as “stranded turtles” with the understanding that we are excluding live turtle strandings.

The developed model depends on the assumptions that stranded turtles died at-sea, were able to float freely (i.e. not entangled), and the stranding event was reported and documented shortly after beaching on land. Carcass decomposition state at time of discovery on the beach is recorded on a condition code scale from 1 to 5, with lower condition codes indicating a “fresher” carcass that likely drifted for a shorter amount of time. Based on experimental results that turtles are positively buoyant and capable of drifting only until code 3 (Chapter 1), stranding events with condition codes 4-5 were

omitted from analyses as beach time to decay to these states is difficult to determine and open ended. Thus, analysis of stranding data was limited to turtles within the model domain and classified as condition codes 1-3 (n=1023).

We also limited analyses to strandings documented on the coastlines within identified regions of high human population densities, with the assumption that strandings in these areas are reported in a timely manner (n=751; 73%). This included stranding events documented along the coasts of Virginia Beach, Norfolk, and bay-side Northampton County (Fig. 1a). The ocean-facing coastline of Northampton County is made up of uninhabited barrier islands that are difficult to access, thus strandings in these areas were omitted from analyses (n=22; 2.2%). We also excluded strandings located up small tributaries and other waterways, for these water areas are not well represented in the oceanographic model and the assumption of observation within 24-hours likely does not hold true (n=20; 2.0%).

From this subset, we focused on strandings occurring during the spring and summer/early fall stranding season (n=651; 87%). Due to lethal water temperatures, turtles are not present in the bay during the winter. Turtles that are documented stranded during this non-residency period either died considerably before being observed or drifted over long times and distances from the open ocean into the bay, both of which complicate estimating their probable mortality locations.

Criteria for a “successful” stranded particle

Three basic conditions were established to determine which particle trajectories potentially correspond to the drift pathways of a stranded turtle, including: 1) arriving within the stranding target area, 2) arriving within a 24-hour time period around the

documented stranding event, and 3) having the appropriate state of decomposition (Table 1).

A target zone was created around the geographic location of each stranding event. Stranding coordinates were snapped to the coastline of the model domain and a target zone with a water area of 28.3 km² was created around each stranding location. This area is equal to the area of a 3 km radius circle, but the actual offshore extent of the buffer around each stranding location was varied so that the water area was constant across strandings after taking into account differences in coastline morphology. Carcass drift simulations were run targeting these specific individual target zones before and up to the date of the corresponding strandings.

To minimize ambiguity regarding potential decay rates of turtle carcasses on land after beaching in areas with low human population densities, simulations were subset to only those stranding events documented along the coasts of Virginia Beach, Norfolk, and bay-side Northampton Counties (Fig. 1a). Virginia Beach and Norfolk are highly inhabited areas and popular summer vacation spots, where waterfront areas are frequently visited in the warmer months. Strandings in these counties were assumed to be observed and reported by a member of the public at least once a day, ranging from approximately 6am to 6pm EST (local time) (Nero et. al 2013). Although Northampton has a lower population density, visitors frequently walk the beaches during the popular summer months, particularly along the bay side of the peninsula where most strandings were reported. Thus, it was assumed that beaches in this area were also observed once every 24-hours. Therefore, we assumed that the actual beaching event in these areas could have occurred anytime from 6pm the night before to 6pm the day of the reported stranding.

This 24-hour duration was used as the stranding window for simulations, with “competent” particles arriving in the stranding target zone during this time period considered to have “successfully” stranded.

Particle tracking times were based on results of a carcass decomposition study (see Chapter 1 for experimental methodology), with water temperatures along particle trajectories and the carcass condition code being used to determine drift duration. In the carcass decomposition study (Chapter 1), eight fresh dead turtles were tethered nearshore and qualitatively assessed every 24-hours to associate reported condition codes with a probable post-mortem interval and estimate oceanic drift duration. Turtle carcasses will only remain buoyant for a limited amount of time, until deteriorating to a point where they are no longer intact enough to retain internal gases and they sink to the bottom. Thus, drift duration of carcasses is limited to the interval of positive buoyancy at a given temperature. Linear regressions were used on buoyancy and condition code results for the eight turtle carcasses to determine the minimum and maximum duration a floating carcass spends in each condition code at a given water temperature (Fig. 2). As turtles in code 1 were not observed buoyant in the study, code 1 turtles were assigned a maximum drift duration of 1 day (similar to Nero et. al 2013), and drift duration for turtles with condition codes 2 and 3 were increased by 24 hours relative to raw results from the decomposition study.

Each model pseudo-particle had a minimum and maximum drift time during which the particle was considered to be buoyant and of the observed condition code for the corresponding stranding. If temperatures were constant over space and time, then the minimum and maximum drift times would be exactly those described (Fig. 2). However,

as temperatures vary, the advancement of a particle towards the minimum and maximum drift duration over a model timestep was assessed as equal to the fraction of the minimum and maximum drift times that the timestep represents for the temperature at the particle location. These fractions were cumulatively summed over timesteps until the total fraction for minimum drift time was >1 , but the total for maximum drift time was <1 . This defined a “competency” window for each particle trajectory during which the carcass was considered to be of the appropriate decomposition state to strand. Particles were then assessed to see if they were within the stranding target zone during this time interval.

Simulations were run targeting each stranding zone individually and starting points of “successful” stranding particles were mapped on a 5 km x 5 km grid. For each stranding, a relative particle density was calculated for each grid cell representing the estimated probability that the turtle died in that grid cell. For each release event (occurring every 3 hours), the number of particles released in each grid cell that successfully landed in the stranding zone at the appropriate time was divided by the total number of particles released in that grid cell to get the relative probability of “successful” stranding. These relative probabilities were then summed over all release events and the resulting sum for each grid cell was further divided by the sum over all grid cells so that the total probability of mortality over all grid cells for a given stranding event was 1.

Analyses

Probable mortality locations for individual stranding events were aggregated over the six year study period by time period and/or stranding type to develop synthetic maps of recurrent mortality locations. Strandings occurring during the spring peak and

throughout the rest of the summer stranding period were analyzed separately. The timing of the spring peak period was independently assessed for each year by plotting the number of strandings per week and visually identifying the sharp peak in strandings in May, indicating onset, followed by a sharp drop off during June, representing the end of the peak period approximately 3-5 weeks later. The duration of the remaining summer and early fall foraging season was defined in a similar manner to encompass the time period after the end of the spring peak until the frequency of stranding events greatly diminished around October or November. This period varied by year from 19 to 23 weeks (Fig. A1).

To assess changes in carcass drift duration throughout the stranding season, timespan and distance from point of release to the first timestep upon entering the stranding zone was recorded for each “successful” stranding particle for all stranding events. Given the variability in drift criteria across condition code, we limited this analysis to strandings classified as condition code 3 to observe trends at the maximum range (results for condition code 2 strandings were qualitatively similar). Average drift times and distances per stranding were binned by week of the year and averaged together over the 6-year study period.

Probability maps of turtle mortality locations were further categorized by probable cause of death as determined by necropsy results and external visual observations of the stranded turtles. Categories examined include vessel strike (n=250; 38%), no apparent injuries (n=163; 25%), and unable to assess (n=199; 31%). Turtle carcasses classified as “no apparent injuries” includes those turtles that appear to have been completely healthy prior to death, while “unable to assess” is comprised of

stranding events with insufficient information (i.e. evaluated by an unqualified observer, necropsy was not performed, etc.) to determine probable cause of death category. The remaining 6% of strandings (n=39) include carcasses with death attributed to disease, cold-stunning, pollution/debris, disease or entanglement. Due to low sample size and diversity surrounding potential causes of mortality, these strandings were excluded from analyses.

Spatial overlap between predicted mortality locations of vessel strike turtles and U.S. Coast Guard shipping lane data were evaluated to assess model validity and identify areas of high mortality due to vessel traffic. Vessel location data from the Automatic Identification System (AIS) for commercial vessels were obtained during the 2009-2014 time period at 1-minute intervals (<https://marinecadastre.gov/ais/>). Vessel density was computed for each year-month strata and rasterized on the 5 km x 5 km grid used to predict turtle mortality. Relative probability of boating activity for each year-month was computed by dividing the number of AIS data points in each grid cell by the total number of points over all grid cells for that strata. The predicted mortality location map for each stranding record was multiplied cell-by-cell with the corresponding year-month relative boating activity layer, resulting in a joint probability distribution map, with each grid cell representing the probability that both boating activity occurred and the turtle died in that location. This joint probability map was summed over all grid cells to develop a single indicator of the overlap between predicted mortality locations and boating activity. AIS data from September to November 2014 were incomplete, so vessel strike turtles that stranded during this time period were omitted from analyses (n=18).

In order to assess whether or not the model was successfully predicting the mortality locations of known vessel strike stranding records, a Monte Carlo randomization analysis was performed to compare overlap between boating activity and the predicted mortality locations of these strandings with the overlap for a randomized mortality location probability map. For each individual stranding event, the model-predicted probability map was randomly reshuffled over the area of all possible mortality locations of turtles for the corresponding year, resulting in a randomly distributed probability map. Similar to the model predicted maps, the randomly generated mortality grids were multiplied by the boating activity map and summed over all grid cells to obtain an indicator of the overlap between these two maps. This process was repeated 5,000 times for each individual stranding event. A pseudo-p-value was calculated as the fraction of these 5,000 trails for which the model predicted had a lower overlap with vessel activity than the randomly distributed null maps. These pseudo-p-values were then aggregated by stranding condition code and plotted as a density function.

Predicted mortality locations for stranding records with probable cause of death classified as “unable to assess” and “no apparent injury” were identified and spatially compared to data on anthropogenic activities. Total harvest for different gear types throughout the Chesapeake Bay were obtained from the Virginia Marine Resource Commission (VMRC) for the 6 year study period. Due to privacy and data resolution issues, harvest was only available as an aggregate over the entire study period and for individual “waterways”, marine areas defined by VMRC and used for harvest reporting by fishermen (Fig. A2). Gear types that are thought to pose particular threats to sea turtle, including gillnets, haul seines, and pots and traps were subset and mapped by waterway.

To ensure confidentiality in cases where the number of harvesters per gear-waterway combination was low, results for certain water areas were grouped together by “water system” (a larger area defined by VMRC to include multiple nearby waterways). In the 10% of instances where this occurred, total pounds harvested per gear-waterway strata was estimated by dividing the gear-water system total among the number of waterway represented within the grouping. Fine scale pound net and stake gillnets locations were obtained from the VMRC website for 2017, the current license year at the time of the study (https://webapps.mrc.virginia.gov/public/maps/chesapeakebay_map.php). Point locations were extracted and plotted on the 5 km x 5 km grid by length of net per unit area. Although fine-scale information on staked gillnets and pound nets locations were only available for 2017, these are stationary, semi-permanent fishing gears that likely remain in the same general area over many years. In addition, this point license location information matches relatively well with available broader-scale information on aggregated 2009-2014 harvest (Fig. A3). Therefore, the gridded 2017 stake gillnet and pound net locations were deemed appropriate to use for comparisons with the 2009-2014 data. Location of purse-seine sets by Omega Protein vessels from 2011-2013 were obtained from the 2015 Atlantic Menhaden Stock Assessment Report (SEDAR 2015). Images of set locations were georeferenced and digitized in ArcGIS, and presence/absence of purse seines noted on a 5 km x 5 km grid.

RESULTS

Possible drift time for strandings classified with condition codes 2 and 3 decreased with warming water temperature (Fig. 2). The effect of temperature was found

to be statistically significant on the maximum drift time for code 2 turtles ($p < 0.001$, $R^2 = 0.7495$) as well as the minimum ($p < 0.01$, $R^2 = 0.7947$) and maximum ($p < 0.001$, $R^2 = 0.8932$) drift times for code 3 turtles (Table 2).

Average drift times and straight-line distances for pseudo-particles successfully arriving at condition code 3 stranding target zones decreased throughout the late spring (May-late June), reached minimal values of ~2-5 days and ~15-30 km, respectively, during the summer months (late June-late September) before increasing again in the fall (late September-November) (Fig. 3a-b). The minimum in both drift times and distances occurred in July, shortly after the spring peak period. A significant relationship was noted between drift time and drift duration (Fig. 3c; $p < 0.001$, $R^2 = 0.2746$).

Although predicted mortality locations differed among probable cause of death categories, as well as between spring peak and summer, non-peak stranding time periods, high probability zones for mortality are consistently identified in areas within the main channel of the lower bay, as well as the James River (Figs. 1b, 4-6). Mortality locations for vessel strike strandings are largely concentrated in the southwest portion of the bay, while most probable locations for strandings classified as no apparent injuries or unable to assess are generally more dispersed and also include areas in the southeast quadrant of the bay. In all cases, mortality is less likely to occur up tributaries of the Bay, with a notable exception of the James River.

Vessel strikes

Analysis of commercial vessel density data highlight high boating activity during months with observed stranding data in the lower Chesapeake Bay, particularly along shipping channels of bayside areas of Norfolk and Virginia Beach and within the lower

James River (Fig. 4a). Overall predicted mortality locations of sea turtle strandings with evidence of death by vessel strike are concentrated in the lower, southwest portion of the Chesapeake Bay (Fig. 4b). In particular, high probability is noted near the mouth of the James River and the bayside coast of Norfolk. Mortality is also moderate to high near the bayside coast of Northampton County, near the mouth of the Bay, and in the northern oceanic-coast of Virginia Beach. A combined probability map depicting overlap of both boating activity and predicted vessel strike turtle mortality is very heavily weighted towards the immediate vicinity of the Lynnhaven Inlet and Elizabeth River (Figs. 1b, 4c).

Results from the Monte Carlo randomization analyses show a strong distribution of low p-values across all condition codes, indicating that the model is doing considerably better than random at predicting vessel-strike mortality event locations (Fig. 7). Actual predicted mortality locations derived from the model is better ($p < 0.05$) at predicting overlap with vessel activity than expected by random chance for approximately 67% of code 1 turtles (4 out of 6 strandings), 54% of code 2 turtles (83 out of 155), and 42% of code 3 turtles (30 out of 71).

No apparent injuries and unable to assess

Predicted mortality locations for strandings classified as “no apparent injuries” or “unable to assess” generally occur throughout the lower bay, with noted differences in probable mortality locations between the spring peak in strandings and the rest of the summer stranding period (Figs. 5-6). Turtles classified as condition code 1 originate in nearshore areas relatively close to stranding locations. Although sample size is low, elevated concentrations are noted near the bayside coasts of Virginia Beach and Northampton. There were no documented code 1 “unable to assess” strandings during the

non-peak stranding period. During the spring peak, predicted mortality locations for turtles classified as both condition code 2 and 3 are heavily concentrated within the James River and along Northampton's bayside coast. Additionally, there is a strong likelihood of mortality near Hampton County (Fig. 1b) for condition code 3 turtles classified as "no apparent injuries" that is not present in any of the other images, with elevated mortality probability strongly concentrated in a region spanning across the lower main-stem of the bay. Non-peak stranding mortality locations are generally more diffuse in space, with high probability mostly near the bayside coast of Northampton.

Wind forcing

Although major areas of predicted mortality remain the same between 0%, 2%, and 4% of wind forcing on carcass drift, increasing winds has a general tendency towards increasing the spread and geographic range of predicted mortality locations (Fig. 8). For example, predicted mortality locations for turtles classified with a condition code of 2 and no apparent injuries during the spring peak depict an elevated probability of mortality near the southern bayside coast of Northampton that is most prevalent with 0% wind forcing and becomes smaller at 2% and 4% (Fig. 8). However, an area of high mortality remains constant within the lower southwest portion of the Bay and the James River across all three wind speed percentages. The high likelihood of mortality occurring in this area across all wind conditions assessed is further highlighted in a map depicting the mean of these three probability images (Fig. 8d).

Fishing data

Focusing primarily on those gears and fisheries that are most active in the lower bay and James River locations predicted to be associated with turtle mortality leading to

strandings (Figs. 5-6), we find that areas of activity of sink/anchor gillnets (as well as drift gillnet to a lesser extent; Fig. 9a-b), haul seines (Fig. 9c), crab pots and traps (Fig. 9e), and the purse-seine fishery for Menhaden (Fig. 10a) overlap extensively with areas of predicted mortality. Nevertheless, the limited spatial and temporal resolution of the data make quantitative assessments of overlap impossible. Of the fixed gears, only pound nets locations (Figs. 10c) correspond with some of the predicted turtle mortality locations along the bay side of Northampton County. Whelk pots and traps (Fig. 9d) and sink gillnets (Fig. 10b) are located in regions of the upper bay or oceanic waters outside the Bay, areas generally do not greatly overlap with predicted turtle mortality locations.

DISCUSSION

In this study, we developed the first model for predicting mortality locations from sea turtle strandings in Virginia, USA, using a methodology that is widely applicable to stranding data for sea turtles and other charismatic megafauna around the world. The novel approach used in our model incorporates wind, current, and temperature effects on carcass drift to stranding locations. We identified probable mortality locations for different categories of strandings in the Chesapeake Bay, making comparisons between high-probability areas with available information on fisheries activity and commercial vessel traffic. Identified hotspots during both the spring peak and summer non-peak stranding season are primarily in two distinct regions within waters of the lower bay: near the vicinity of the James River and lower bay-side coast of Northampton County.

Vessel strikes

Combined probability maps of vessel density and predicted mortality locations for vessel strike turtles suggest that watercraft interactions leading to mortality occur primarily in the lower Chesapeake Bay just north of Virginia Beach in the vicinity of the Lynnhaven Inlet, as well as in the James River near the Elizabeth River (Fig. 4c). Given the importance of the Norfolk and Virginia Beach areas for commercial, recreational and military maritime traffic, turtle-vessel interactions are to be expected. Sea turtles are susceptible to interactions with boating activity throughout their entire range, with vessel strikes identified as an important mortality factor in several nearshore turtle habitats worldwide (Orós et al. 2005, Chaloupka et al. 2008, Casale et al. 2010). In Virginia, loggerheads appear to be particularly affected by vessels and rarely survive propeller trauma (Barco and Swingle 2014). Barco et al. (2016) note that the majority of loggerheads that strand in the Bay with vessel damage represent normal, healthy turtles prior to interactions, which suggests that mortality occurs as a direct result of lethal vessel-turtle contact. Our results complement this information by providing precise target areas for mitigation efforts to reduce probability of lethal vessel-turtle interactions.

Overall, analysis of vessel strike mortality location predictions suggest that our model is a good predictor of locations with high likelihood of human interactions. Our Monte Carlo randomization analysis indicates that mortality location predictions overlap boating activity maps far more than one would expect at random (Fig. 7). Based on the overlap with boating activity, the drift model is best at predicting mortality locations for stranded turtles classified as condition code 1, followed by code 2 turtles then code 3 turtles. This is as one would expect, for turtles found in a code 1 condition are freshly

dead and have likely had only a short amount of time to drift before stranding, leading to lower uncertainty in their drift trajectory.

Although the analysis of turtles with evidence of death by watercraft interaction provide a good proxy for assessing model accuracy, the nature of the AIS boat position data may underrepresent and/or misrepresent overall vessel activity in the bay. AIS provides a vast amount of real-time vessel track data, but is only legally required for certain larger vessel types, including large commercial vessels and industrial fishing vessels (Title 33, Code of Federal Regulations, Part 164). The data do not account for smaller commercial vessels and recreational vessels. Furthermore, all vessels owned and operated by the U.S. government are legally exempt from AIS data reporting requirements (Title 33, Code of Federal Regulations, Part 164). The Chesapeake Bay has significant military ports, including, but not limited to, the Norfolk Naval Base, the largest naval base in the world. Therefore, identified regions of high vessel activity underestimate both the intensity and spatial distribution of vessel activity in the study area. These differences between available data and the real distribution of vessel traffic in the bay likely explain the fact that model mortality location predictions for a small number of vessel strike turtle strandings did not extensively overlap vessel traffic data (e.g., if the strike was caused by a recreational vessel outside of normal shipping channels; see pseudo-p-values > 0.5 in Fig. 7).

Potential fisheries interactions

The distribution of sink/anchor gillnets, crab pots, and purse seine fishing overlap with both distinct areas of high probability of sea turtle mortality: the lower James River region and bay-side Northampton coast (Figs. 5, 6, 9-10). Mortality of both loggerhead's and Kemp's ridley have been observed within Virginia's gillnet fisheries (Turtle Expert

Working Group 2000, Mansfield 2006), and it has been suggested that large-mesh gillnets used in monkfish, black drum, smooth hound fisheries within the bay may pose a threat to sea turtles (Mansfield et al. 2001). Sink gillnets in the nearshore waters of the bay may interact with bottom-feeding turtles as they forage for food. Crab pots pose a threat to turtles through entanglement with vertical lines, but a side scan sonar survey conducted during the 2006 spring peak of turtle strandings found no entanglements in any of the over 1,600 crab or whelk pot gears monitored (DeAlteris Associates Inc 2006). Menhaden purse seine effort overlaps with nearly all probable mortality locations, with the notable exception of the region of high mortality likelihood in the James River (Figs. 5-6, 10a). However, results from a 1992 study investigating bycatch in the mid-Atlantic menhaden fishery found no sea turtles captured or even observed during sampling, as well as particularly low bycatch within the Chesapeake Bay fleet (Austin et al. 1994). Nonetheless, high overlap of fishing activity with multiple regions of high mortality probability suggest these fishing gears may contribute to sea turtle mortality to some degree.

The concentration of haul seine effort almost exclusively in the southwest quadrant of the bay align with predicted mortality locations near the James River and coastline of Hampton County (Figs. 5-6, 9c), while high drift gillnet activity in the southeast region of the bay coincide with some of the probable mortality locations near Northampton County (Fig. 9a). Haul seines pose a threat to sea turtles through forced submergence, and have been documented to incidentally capture sea turtles within Virginia (Lutcavage 1981). Similar to sink/anchor gillnets, drift gillnets may pose a

hazard to sea turtles through entanglement in gear with large mesh sizes. Therefore, these gear types cannot be omitted as potential drivers of mortality to sea turtles in the bay.

Minimal overlap is noted between probable mortality locations with whelk pots and traps, staked gillnets, and pound net gear (Figs. 5-6, 9d, 10b-c), suggesting it is unlikely that interactions with these fisheries result in large numbers of sea turtle mortalities. Although some likely mortality locations coincide with pound net usage in the northwest bay, a number of regulatory changes relating to use of modified pound net leaders were made to this fishery in the mid-2000s specifically to reduce turtle mortality (67 FR 41196, 69 FR 24997, 71 FR 36024, 73 FR 68348). Research suggests that these regulations have resulted in a significant reduction of pound net turtle entanglements (Dealteris and Silva 2007, Silva et al. 2011).

This study highlights novel methodology that significantly improves our ability to identify likely locations of sea turtle mortality. However, a complete quantitative assessment of overlaps between anthropogenic activities and these turtle mortality location predictions is limited by the poor spatial and temporal resolution of fishing activity data available for comparisons. Somewhat unusually, this study represents a case where our ability to model the biology (i.e., the drift and decomposition of turtle carcasses) exceeds our ability to interpret model results in light of available anthropogenic observations. For instance, data from VMRC at the waterway level were only accessible as an aggregation over the 6-year study period, prohibiting comparisons on a month-year level. Thus, although there are noted differences in mortality location for the spring peak compared to the remaining of the stranding period, lack of temporal fisheries information makes it impossible to assess differences in potential causes of

mortality for the two different time periods. If data on anthropogenic activities, such as fishing, were available on spatial and temporal scales pertinent for interpreting individual stranding events (kilometers and a week to a month, respectively), then the overlap between these activities and mortality location predictions could be calculated and one could quantitatively assess which activities were most likely to be causing the mortality.

For some human activities, such as commercial boat traffic, detailed information were available and we were able to quantitatively compare and combine these data with mortality predictions. For others, such as the purse-seine menhaden fishery, detailed data exist, but are not currently publicly available due to industry confidentiality, public image and equity (among fisheries) concerns. OMEGA Protein operates the sole menhaden reduction plant along the Atlantic coast since 2005 and controls all purse seine vessels (Kirkley 2011). Due to the single participant in this fishery, purse seine location data was not available from VMRC. We requested data on purse seine fishing locations directly from OMEGA Protein, but our data request was denied due to confidentiality concerns and fear of negative repercussions on the image of the industry. OMEGA Protein's chief scientist highlighted that the observer program for menhaden purse seine operations in the bay has found no evidence of significant interactions with sea turtles, consistent with other studies on menhaden bycatch (Austin et al. 1994). Nevertheless, observers may not see all lethal and sub-lethal interactions between the fishery and sea turtles, and it is an important avenue to consider for future investigations.

Given the endangered status of sea turtles and potential societal and environmental benefits of addressing threats in a timely fashion, these data barriers should be lifted. For still other human activities, such as gillnet and trap fisheries, few

spatio-temporally precise data are currently being collected. Nevertheless, a combination of increased observer coverage, vessel monitoring systems and new, and increasingly cheap, tracking technologies can address these data deficiencies if funds are made available. The availability of data on anthropogenic activities on a finer spatio-temporal scale is key to the ability to conduct more robust identifications of drivers that threaten local sea turtles populations, as well as other charismatic marine megafauna.

Mitigation measures

Slower vessel speeds are noted as the primary tool to reduce vessel damage to sea turtles, as well as other marine mammals (Laist and Shaw 2006, Calleson and Frohlich 2007, Hazel et al. 2007). Speed limitations are especially important in shallow habitats (Hazel et al. 2007), such as the nearshore areas where turtles forage in Chesapeake Bay. According to Hazel et al. (2007), sea turtles cannot avoid vessel collisions unless boats are traveling at less than 4 km/hr, but this is less than idle speed for many vessels. However, using the results from this study, managers can consider strategies for boaters to avoid, minimize travel distance, or reduce speeds in predicted areas with a high likelihood of vessel-strike sea turtle mortality (Fig. 4b) and/or high probability of vessel-turtle interactions during the stranding season (Fig. 4c).

Similarly, management regulations on the fishing industry (i.e. time area closures, limited soak time, etc.) or gear modifications should be prioritized in time and space where there is an increased likelihood of interaction with sea turtles. Energetic demands from spring migrations cause turtles to be weaker and in poor health upon entering the bay, and thus may be at a greater risk of entanglement with fishing gear if caught in strong currents (Bellmund et al. 1987, Byles 1988). In addition, it is possible that turtles stranding during the spring peak are weakened from predisposed condition or cryptic

mortality occurring during their migration into the bay. By the time mortalities drop near the end of June, turtles are able to forage and move around nets with minimal threat (Lutcavage and Musick 1985, Byles 1988). Therefore, from a temporal standpoint, management efforts may choose to prioritize implementing regulations during this vulnerable spring peak time period.

Predicted mortality locations for turtles classified as having no apparent injuries or as unable to assess were noted to differ within the spring peak compared to the rest of the stranding season, generally shifting from the southwest portion of the bay to southeastern waters near the bay-side of Northampton County (Figs. 5-6). Some maps also show a shift in mortality locations from the lower bay to more northern Virginia areas of the bay, consistent with movement of turtles into the bay as the foraging season progresses. Thus, rolling regulations taking into account turtle behavior and distribution during different times of the stranding season could be pursued.

The high rate of strandings during the spring peak has generally been interpreted as indicative of higher sea turtle mortality rates during this period as compared to the rest of the summer foraging season. Nevertheless, it is possible that sea turtle mortality is constant throughout the spring and summer stranding season, but turtles are more likely to succumb to decomposition before making landfall during summer, leading to fewer stranding observations. Turtles decompose at a slower rate in cooler waters (Chapter 1, Higgins et al. 1995), with results from this study suggesting that turtle carcasses have the potential to drift ~2-5 days longer and ~15-30 km further during the cooler spring peak period compared to those turtles dying during the hot summer months (Fig. 3). This difference in drift duration could explain variability in stranding rates during the

spring/summer foraging season, though this hypothesis is difficult to quantitatively assess without knowing more about the spatial distribution of true turtle mortality in the bay. This hypothesis is also consistent with a small fall peak in strandings (Coles 1999, Barco and Swingle 2014), during which time we predict that drift durations should be significantly longer than during the summer. Therefore, although management actions may prioritize mitigation measures during the spring peak period, strong protection of local turtle populations is crucial throughout their entire residency in the bay.

Conclusion

The results of this study provide the first attempt to identify potential causes of sea turtle mortality based on mortality location predictions for Virginia waters of the Chesapeake Bay. Despite data limitations, these results provide ample material for developing focused time-area management measures for reducing sea turtle mortality in the bay. Given the protected status of sea turtles and importance of the Chesapeake Bay for hundreds of turtles each year, targeted mitigation measures are urgently needed to ensure the persistence of local turtle populations. Furthermore, as temperatures increase due to climate change, the Bay is predicted to become much more favorable to sea turtles (Pike 2014), and, therefore, it is extremely important to identify and manage for any anthropogenic causes of mortality now before there has been a significant increase in turtle usage of the bay. Future research and management efforts should focus on obtaining more detailed spatio-temporal data on anthropogenic activities so that the list of potential mortality drivers can be further restricted based on quantitative comparisons between the distributions of these activities and mortality location predictions, as well as on assessing probability of landfall for different areas of the bay so as to estimate absolute turtle mortality rates. The experimental and modeling methods developed here

provide a sound basis for these future efforts, as well as a template for assessing and understanding stranding data for sea turtles and other marine megafauna around the globe.

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TABLE 1. Criteria that must be met for each pseudo-particle to be considered “successful” for a particular stranding event.

Criteria	Description
Stranding window	Pseudo-particle is within the 24-hour stranding window, defined as 6pm the day before to 6pm the day of the reported stranding event (local time)
Stranding location	Pseudo-particle is spatially within the stranding zone, defined as an 28.3 km ² water area around the stranding coordinate so that the offshore extent is equal to the area of a 3 km radius circle
Carcass condition	Pseudo-particle is positively buoyant and has “decayed” to a point where it is considered to be of the appropriate decomposition state to strand

TABLE 2. Linear regression parameters including the y-intercept (Y-int.), slope, and significance (signif.), from the decomposition study, relating temperature with minimum (min) and maximum (max) buoyancy times during condition codes 1-3. Note that the y-intercept has been adjusted by 1 to account for the assumption that code 1 turtles are buoyant for only one day. Condition code 1 and minimum time of buoyancy for condition code 2 is not based on experimental data, thus significance values are not reported.

Time period	Condition code	Y-int.	Slope	Signif.
Min	1	0	0	N/A
Max	1	1	0	N/A
Min	2	1	0	N/A
Max	2	14.99	-0.412	<0.01
Min	3	16.72	-0.50	<0.05
Max	3	29.32	-0.91	<0.01

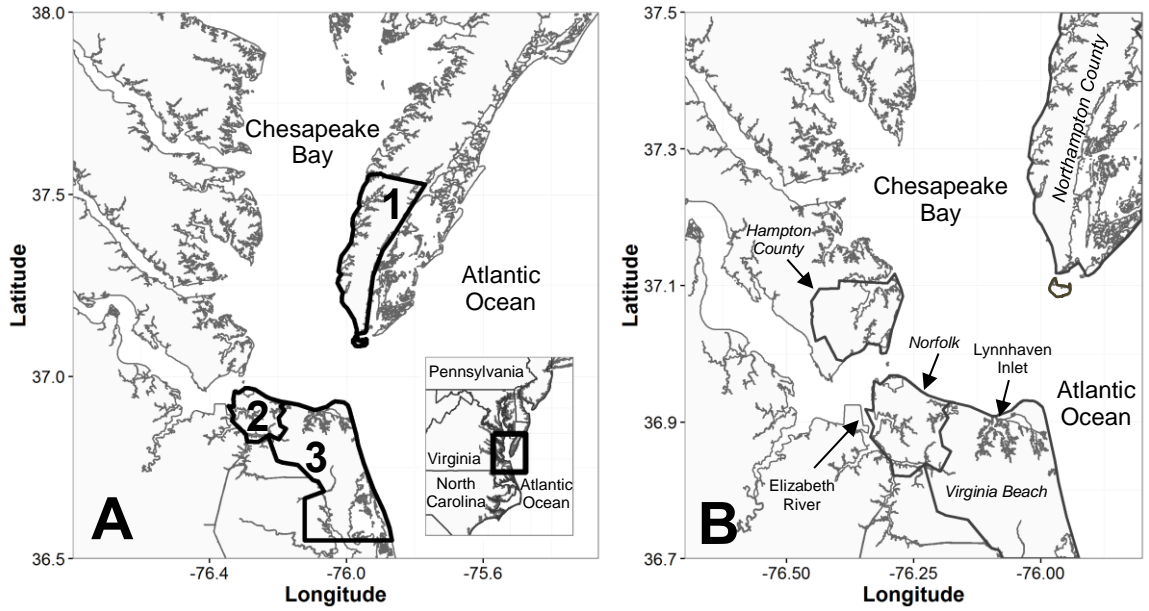


FIGURE 1. (A) Location of top three areas with reported sea turtle strandings in Virginia from 2009-2014, including 1) the bay-side of Northampton County, 2) Norfolk, and 3) Virginia Beach. (B) Expanded view of the lower Chesapeake Bay.

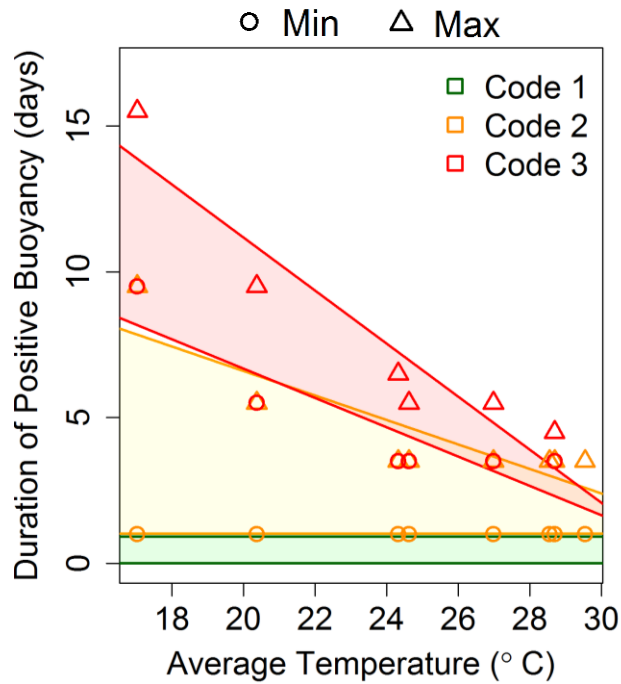


FIGURE 2. Duration of positive buoyancy (days) vs average water temperature (°C) based on results from the experimental decomposition study (Chapter 1). Shaded region represents the time period of positive buoyancy for turtles classified as condition code 1 (green), code 2 (yellow) and code 3 (red). As turtles in condition code 1 were not observed in the study, code 1 turtles were assigned a maximum drift duration of 1 day, and drift duration for turtles with condition codes 2 and 3 were increased by 24 hours relative to raw results from the decomposition study. Individual data points are represented for code 2 turtles (yellow) and code 3 turtles (red), with shapes representing the minimum (circle) and maximum (triangle) duration a floating carcass spent in each condition code. Solid lines represent linear regressions.

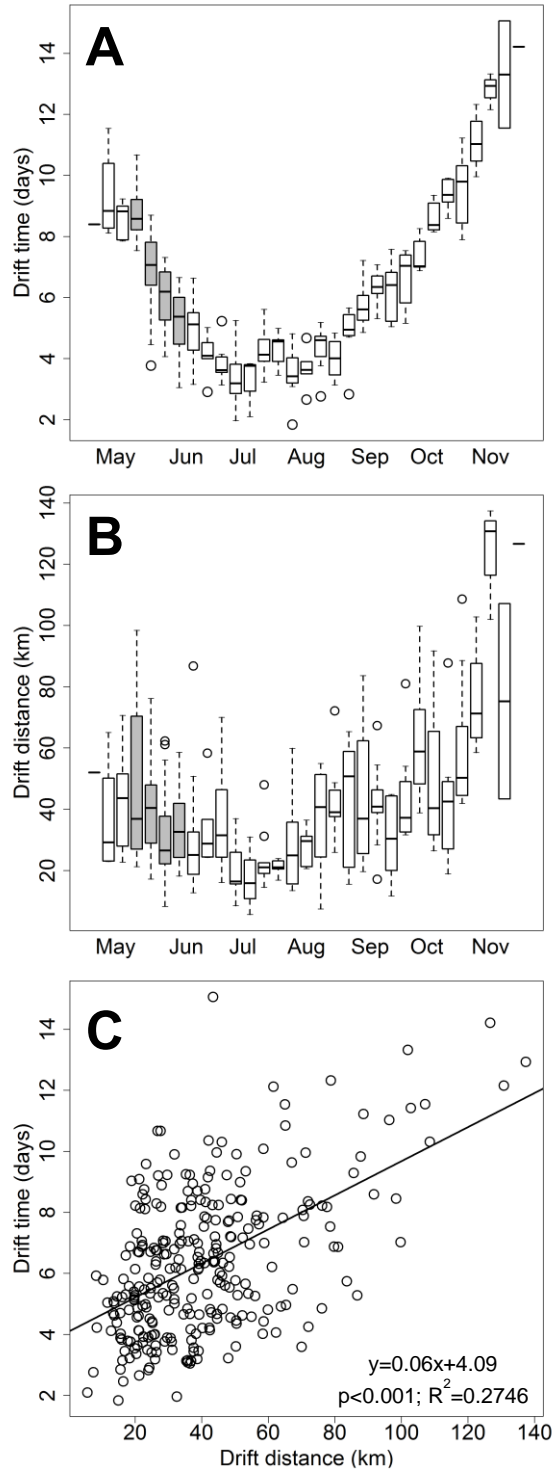


FIGURE 3. Boxplot of average (A) drift times (days) and (B) drift distances (km) of modeled particles leading to a condition code 3 stranding event. Results are aggregated by week of the year with gray-colored boxes representing strandings occurring during the spring peak time period. (C) Linear regression of drift time (days) vs drift distance (km).

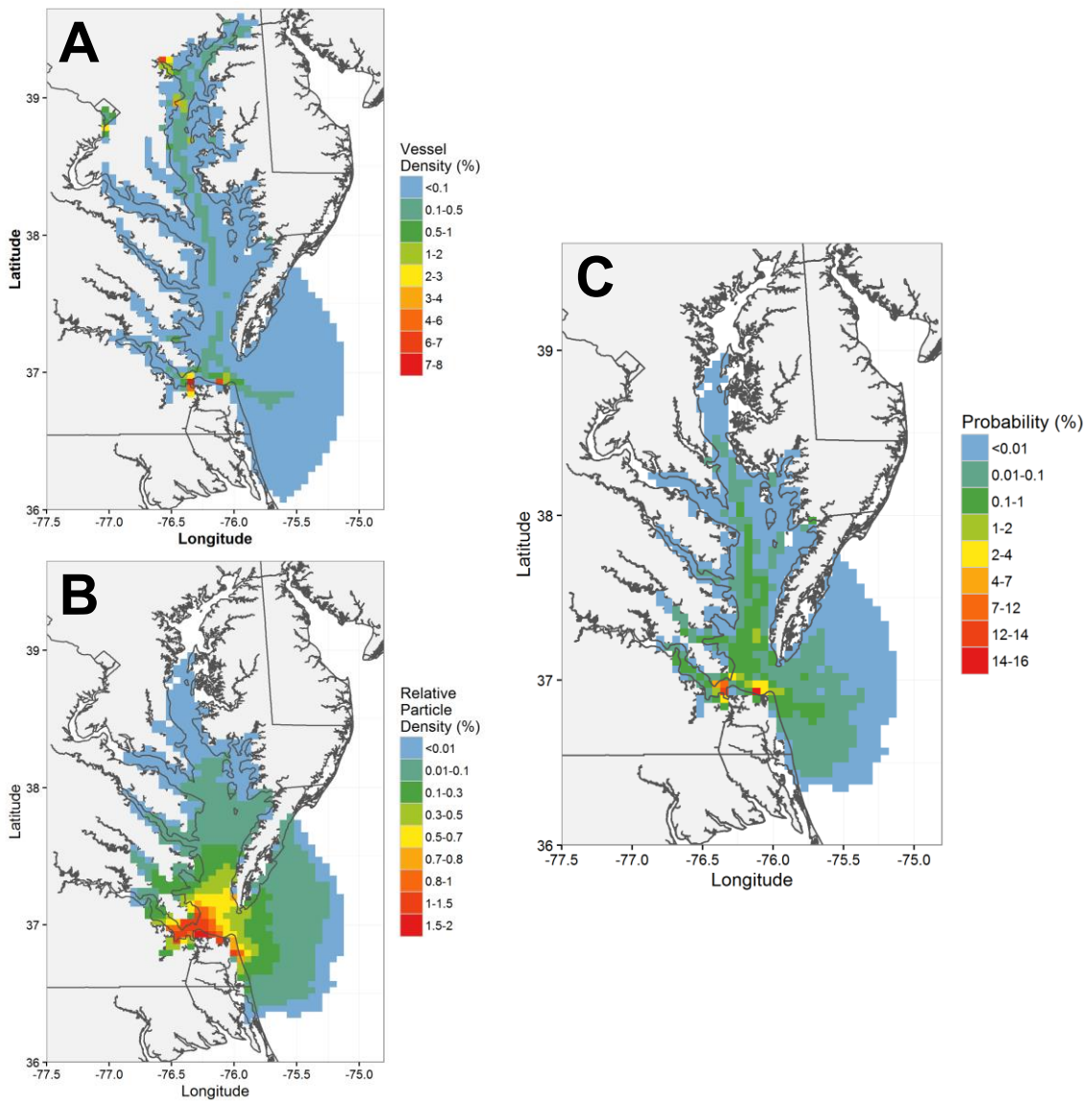
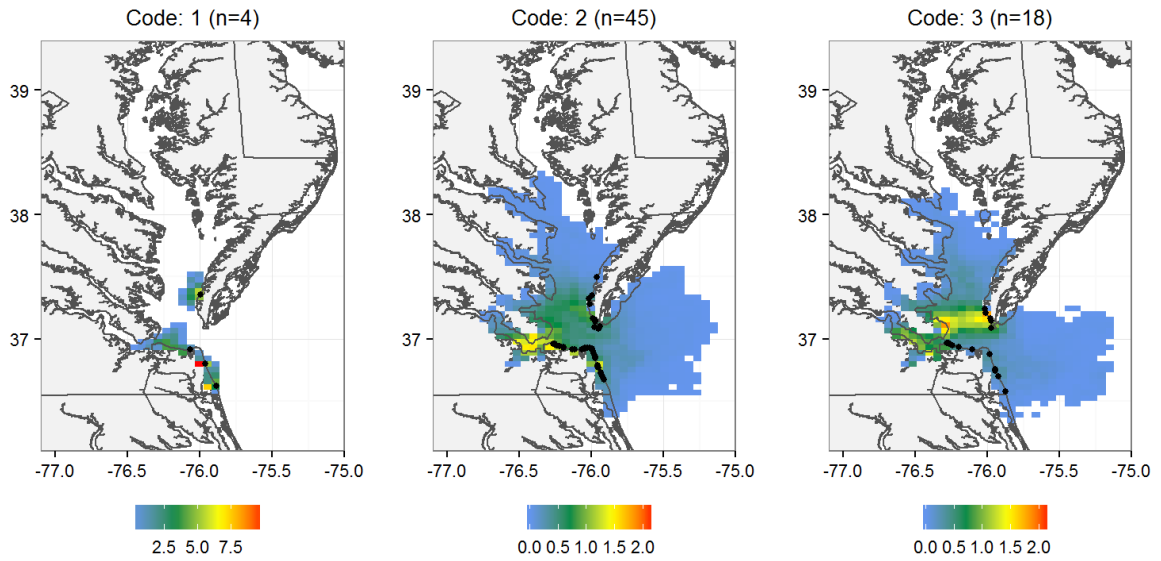


FIGURE 4. (A) Vessel density (%). (B) Relative particle density (%) for probability of point of origin for turtle mortality leading to a stranding and classified with probable cause of death as vessel strike. (C) Combined joint probability (%) depicting the overlap between boating activity and the predicted mortality locations of vessel strike strandings.

Probable Cause of Death: No apparent injuries

(A) Spring peak



(B) Remaining stranding period

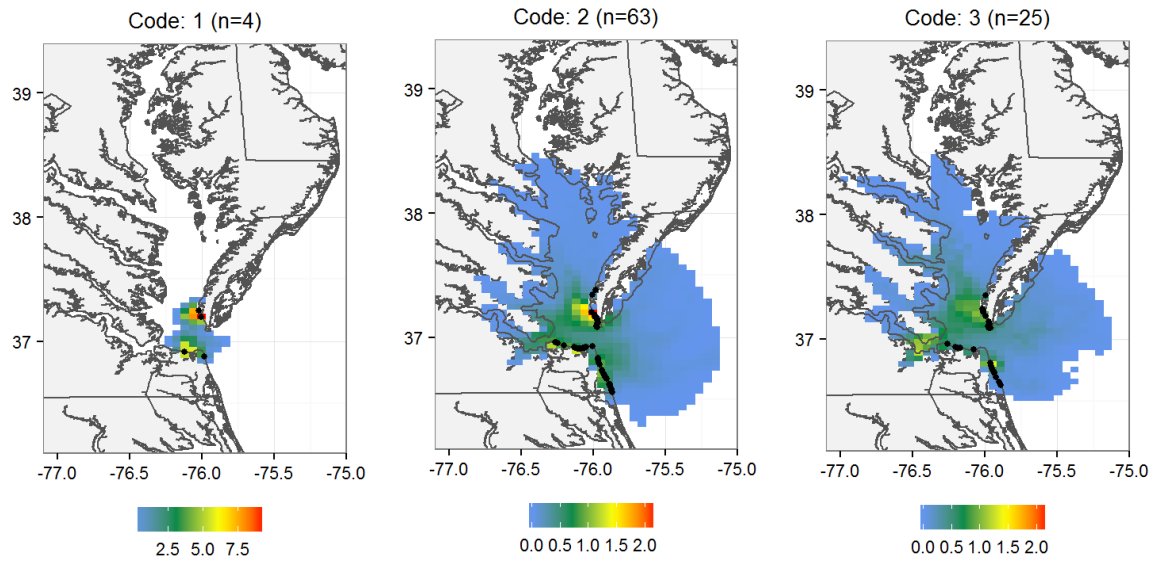
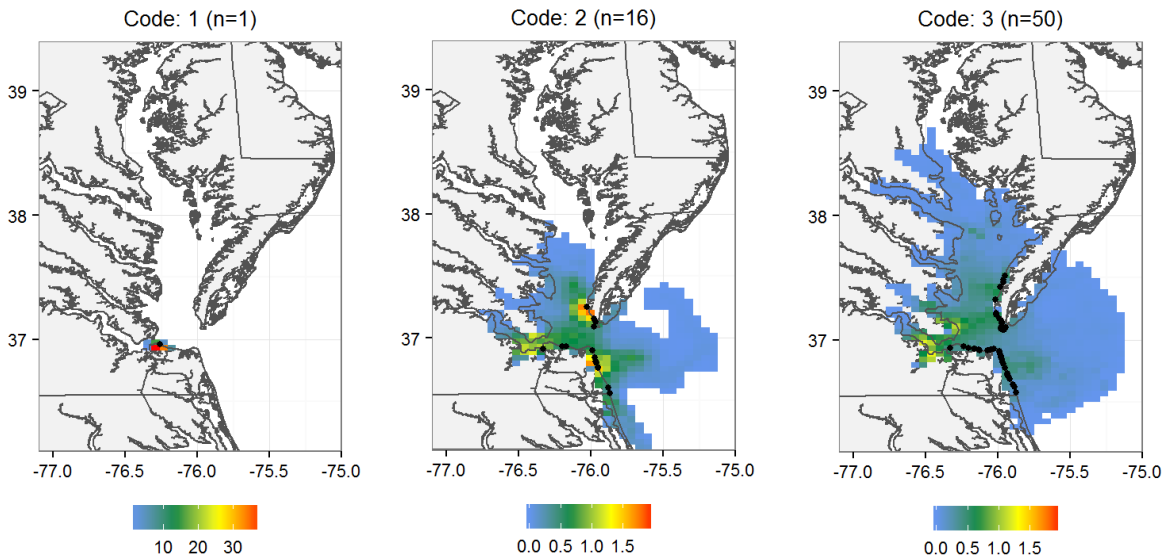


FIGURE 5. Relative particle density (%) for probability of point of origin for turtle mortality leading to a stranding and classified with probable cause of death as no apparent injuries during (A) the spring peak and (B) the remainder of the stranding period. From left to right, panels give results for code 1, code 2 and code 3 strandings, respectively. Note that the scales for codes 2 and 3s have been standardized across time periods.

Probable Cause of Death: Unable to assess

(A) Spring peak



(B) Remaining stranding period

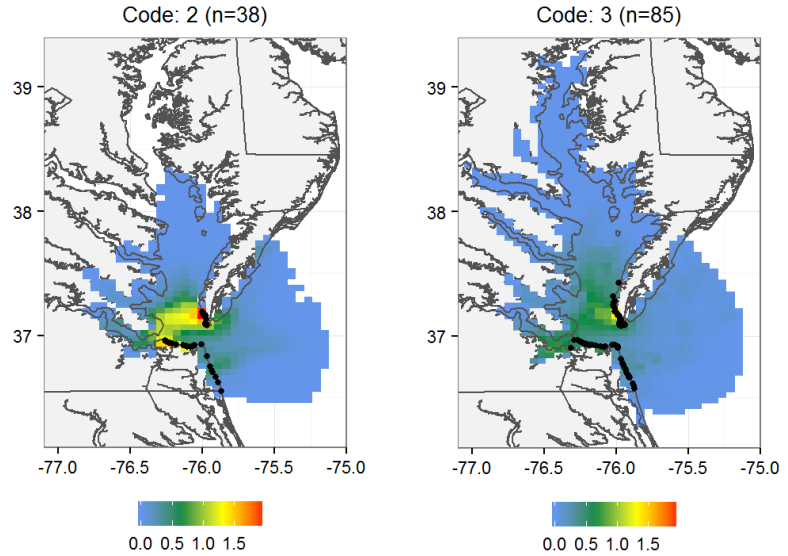


FIGURE 6. Relative particle density (%) for probability of point of origin for turtle mortality leading to a stranding and classified with probable cause of death as unable to assess during (A) the spring peak and (B) the remainder of the stranding period. From left to right, panels give results for code 1, code 2 and code 3 strandings, respectively. Code 1 strandings were only reported during the spring peak period. Note that the scales for codes 2 and 3s have been standardized across time periods. The black outlined box in results for condition code 3 turtles during represents an outlier.

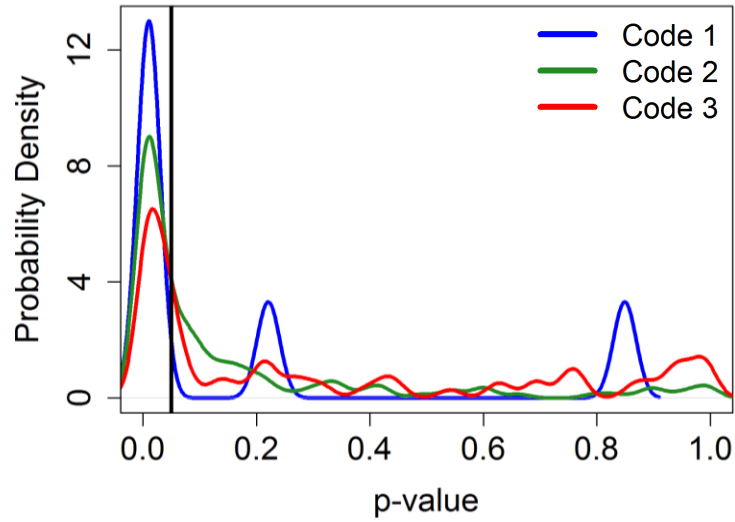


FIGURE 7. Results from Monte Carlo analysis depicting the probability density function that the model is better ($p < 0.05$) at predicting overlap with vessel activity than Monte Carlo randomly distributed null models. Colored lines represent p-values for condition code 1 (blue), 2 (green), and 3 (red). The black solid line represents a significance value of 0.05.

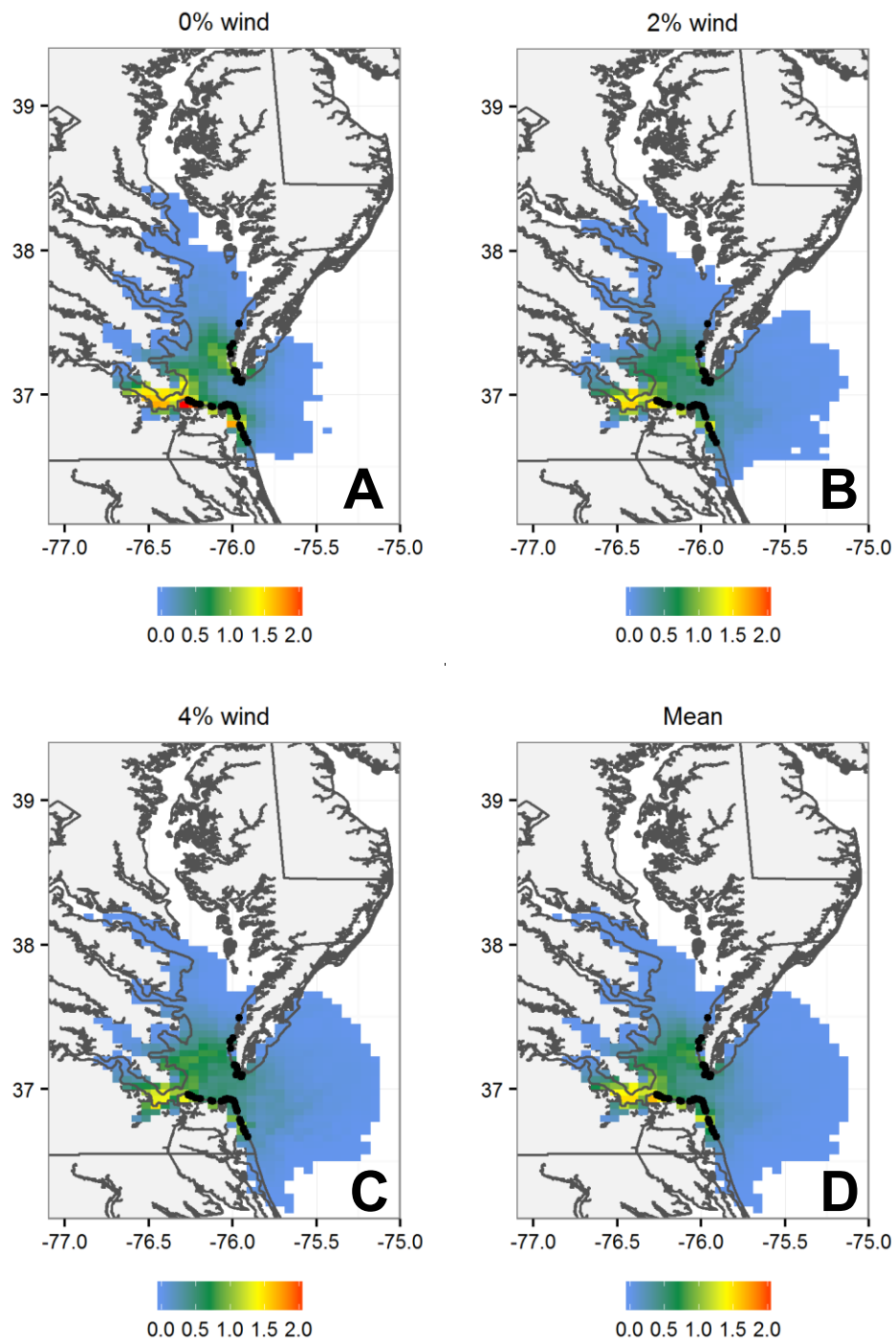


FIGURE 8. Relative particle density (%) for probability of point of origin for turtle mortality leading to a stranding classified as condition code 2 with no apparent injuries during the spring peak. Results include (A) 0%, (B) 2%, and (C) 4% of direct wind forcing on carcass drift, as well as (D) the mean of the results with the varying wind forcing values combined. Note that the color scales have been standardized.

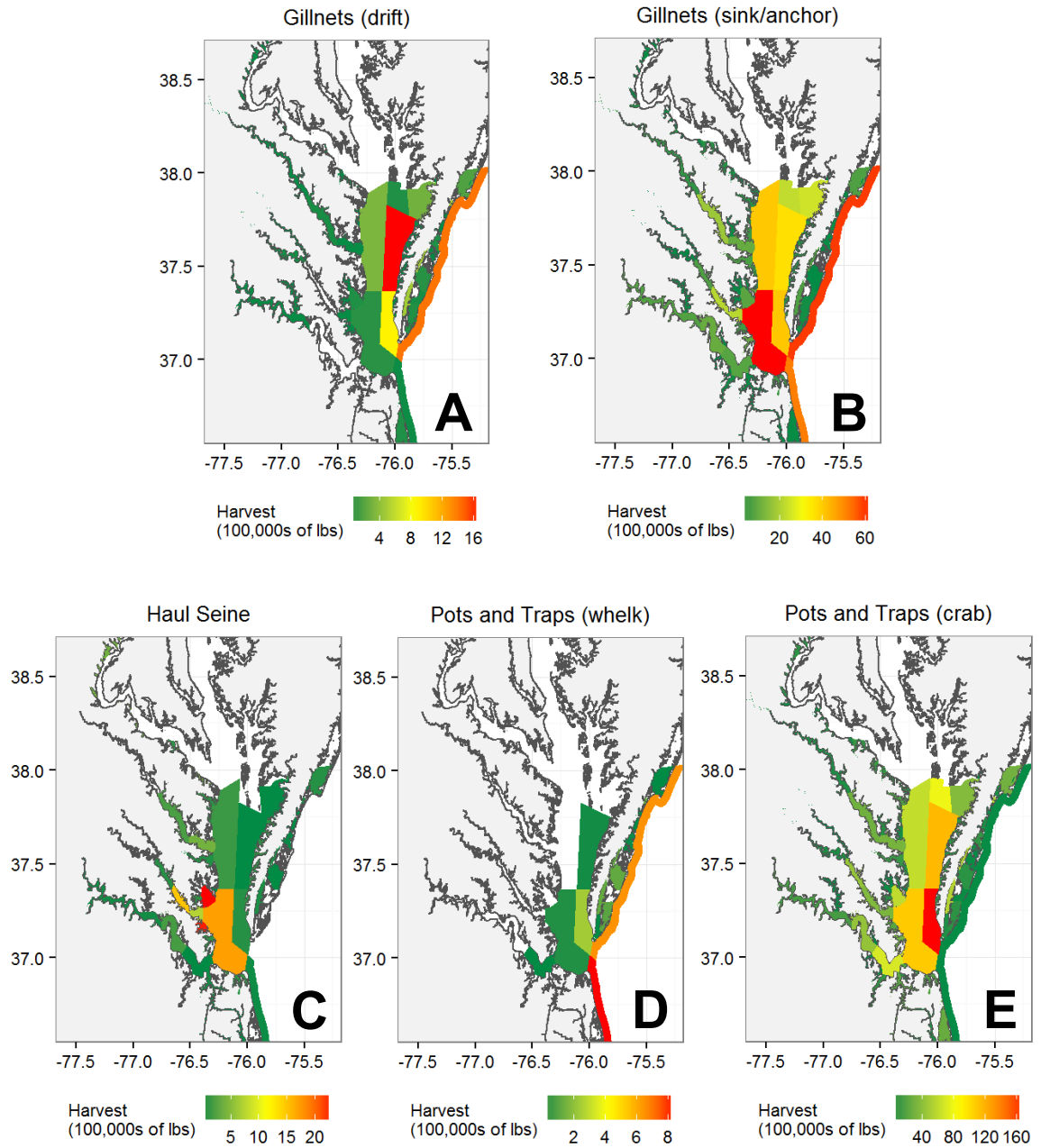


FIGURE 9. Harvest (hundreds of thousands of pounds) by (A) drift gillnets, (B) sink/anchor gillnets, (C) haul seines, (D) whelk pots and traps and (E) crab pots and traps gear. Data was obtained from the Virginia Marine Resource Commission and aggregated over 2009-2014.

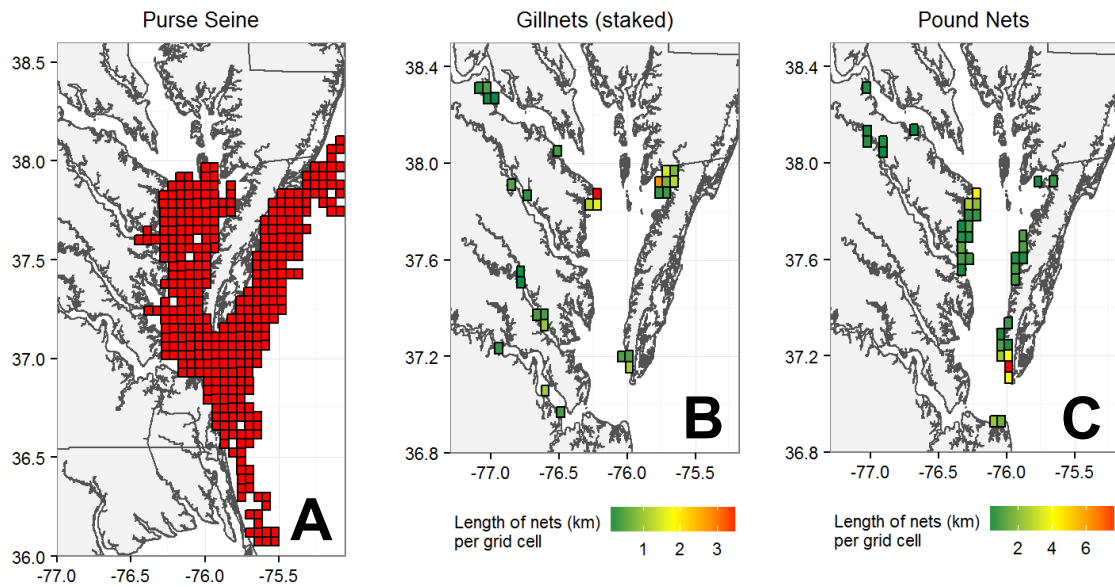


FIGURE 10. (A) Menhaden purse seine sets locations (red) aggregated over 2011-2013, obtained from the 2015 Atlantic Menhaden Stock Assessment Report. Length (km) of net per 5 km by 5 km grid cell for (B) staked gill nets and (C) pound nets based on point locations obtained from the Virginia Marine Resource Commission website for 2017, the current license year at the time of the study.

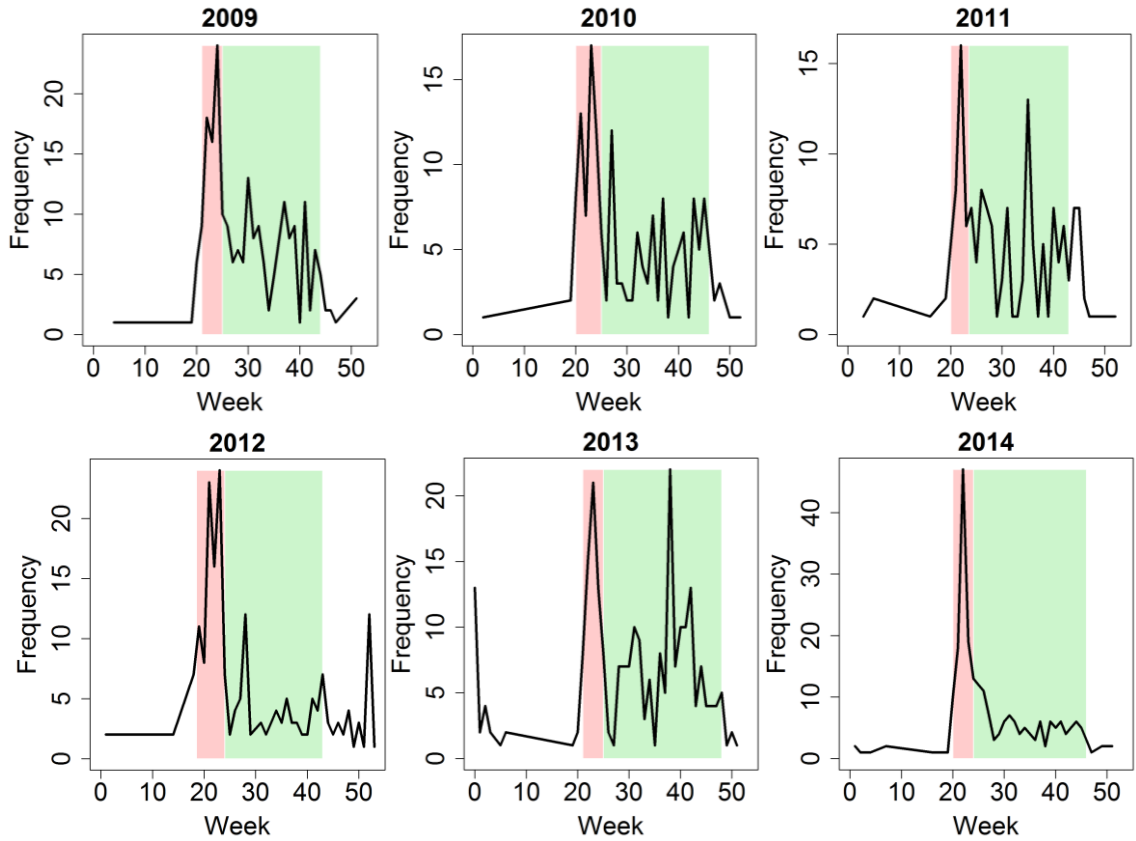


FIGURE A1. Frequency of all reported stranding events per week of the year for 2009-2014. Shaded areas represent the spring peak (red; 3-5 weeks) and the remainder of the stranding period (green; 19-23 weeks).

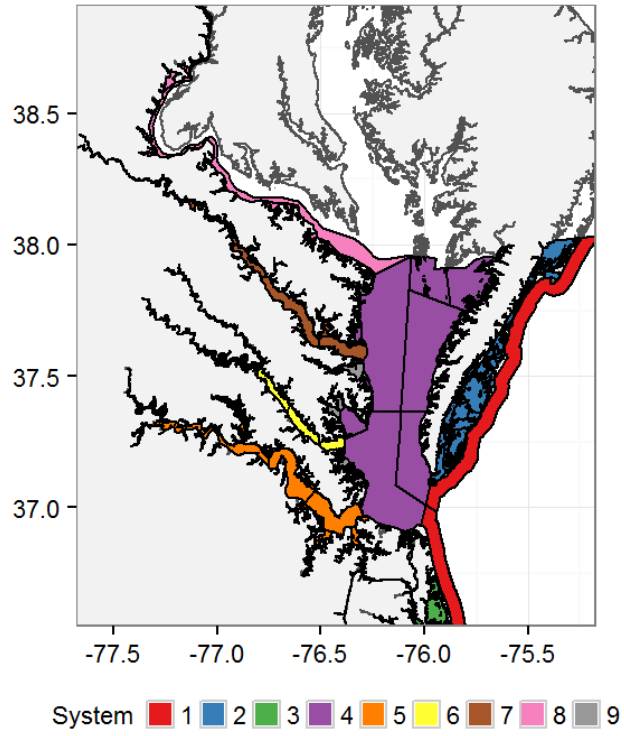


FIGURE A2. Virginia Marine Resource Commission waterways (black outline) and system (color) identification.

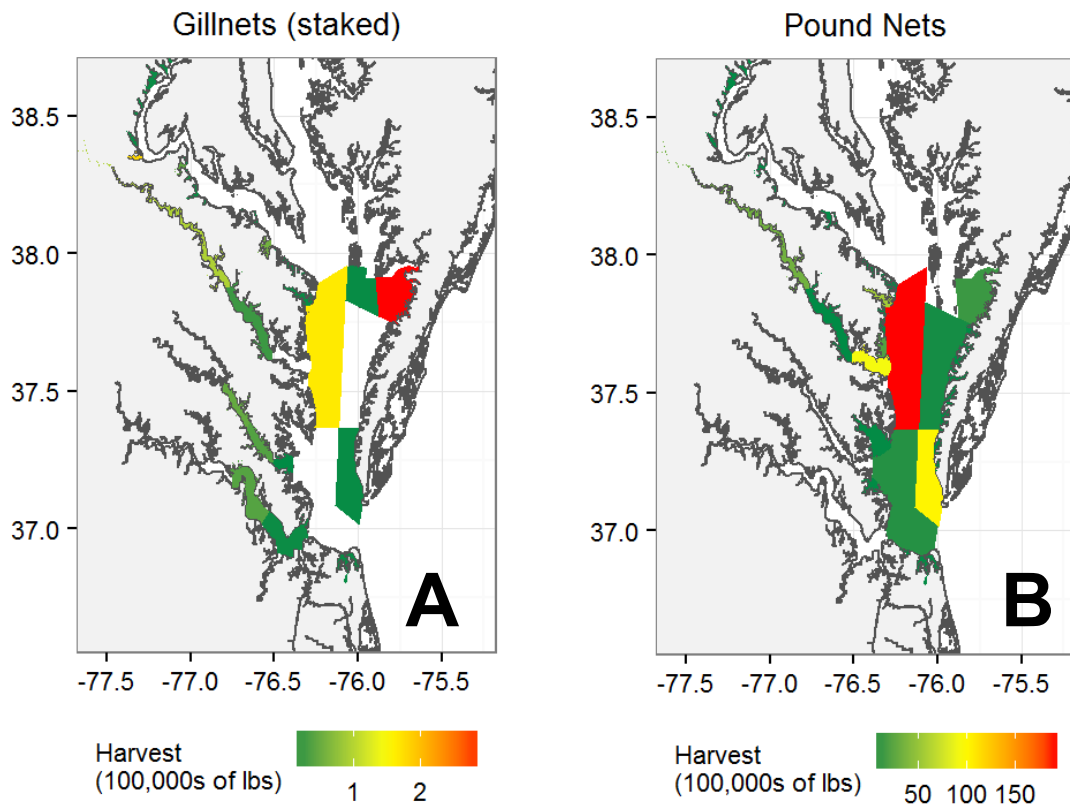


FIGURE A3. Harvest (hundreds of thousands of pounds) by (A) staked gillnet and (B) pound net gear. Data was obtained from the Virginia Marine Resource Commission and aggregated over 2009-2014.

CONCLUSION

The vulnerable state of threatened and endangered sea turtles around the globe has raised concerns in scientific and management communities about population persistence, creating an urgency to better understand and mitigate against mortality events. The overall objectives of this research were to develop an oceanographic drift model for the Chesapeake Bay simulating the drift patterns of dead turtles to stranding locations, and use this model to identify likely locations and mechanisms of sea turtle mortality from stranding records. The methods and model developed in this study will be instrumental for predicting locations of mortality from turtle (and potentially marine mammal) stranding events around the globe, allowing management efforts to focus on alleviating threats in specific geographic areas.

The first chapter of this thesis outlines one of the first systematic efforts to estimate two key parameters needed to model sea turtle carcass drift: probable oceanic drift time and the impact of direct wind forcing on carcass movement. It was found that turtle carcasses drift at 1-4% of wind speed and can decompose within two weeks during Virginia's late spring-early fall high stranding period. Integrating these parameters into an ocean transport model predicting the drift trajectories of turtle carcasses prior to stranding in Virginia, mortality hotspots were identified off coastal southeastern Virginia and within the lower Chesapeake Bay.

The carcass drift model was improved and applied to identifying potential causes of mortality for stranded sea turtles in Virginia in chapter 2. Specifically, the model was used to target specific stranding events, providing a probability map for mortality location for individual strandings that were then aggregated for specific subsets of strandings with similar characteristics. Carcass drift time varied between strandings based

on water temperatures and the observed condition of the carcass at stranding. The specific subsets of 2009-2014 strandings that were analyzed included stranding events classified with no apparent injuries, suggesting mortality could have been caused by fisheries interactions. Predicted mortality hotspots identify consistent areas of high likelihood in the southwest and southeast areas of the bay, which spatially overlap with gillnet, seine, pot and pound net activity. Nevertheless, lack of spatially and temporally varying fishing data limited our ability to quantitatively compare mortality hotspots with fishing effort. Despite this limitation, my predictions for the distribution of sea turtle mortality leading to strandings provides significant new information to inform the development of effective management strategies in focused locations within Virginia's waterways.

This study highlights a number of future developments and improvements to our approach that could significantly enhance our ability to identify threats facing sea turtles in the bay and elsewhere around the globe. Principal among things that could be improved in future research is the sample size of turtle carcasses used in the drift and decomposition studies, as well as the poor spatial and temporal resolution of anthropogenic activities that were available for comparisons with our predicted mortality hotspots. The availability of additional turtle carcasses for the field experimentations would increase the statistical robustness of the data as well as allow for further analyses on the effects of size, species, and environmental conditions. Nonetheless, the results from this study provide one of the first estimates of turtle decomposition rates and wind leeway throughout controlled field studies in the literature. Additionally, somewhat unusually, our ability to model biology (i.e., the drift and decomposition of turtle carcasses) exceeds our ability to interpret model results in light of available

anthropogenic observations. If the availability of anthropogenic activities, such as fishing, were available on spatial and temporal scales pertinent for interpreting individual stranding events (i.e. kilometers and a week to a month, respectively), then the overlap between these activities and mortality location predictions could be calculated, allowing for quantitative assessments of which activities were most likely to be causing the mortality. For example, detailed information were available on commercial boat traffic, and thus I was able to quantitatively compare and combine these data with mortality predictions. However for others, such as the purse-seine menhaden fishery, detailed data exist, but are not currently publicly available due to industry confidentiality and public image. For other human activities, such as gillnet and trap fisheries, little spatio-temporally precise data is currently being collected, yet these barriers can be overcome with a combination of increased observer coverage and new, relatively cheap tracking technologies. Given the endangered status of sea turtles and potential societal and environmental benefits of addressing threats in a timely fashion, such data is crucial to accurately characterizing the impact of fisheries interactions. Furthermore, this study provides detailed predictions of time periods and spatial regions where investment in such technologies and programs is most likely to yield important information for management.

The use of stranding data requires careful consideration in light of the potential in reporting bias. Although strandings provide a detailed dataset to improve understanding of sea turtle mortality in nearshore environments, stranding events are often opportunistic in nature and can be biased due to spatial and seasonal variability in reporting (Hart et al. 2006, Witt et al. 2007). In Virginia, the southeast area of the bay where large numbers of

strandings are reported on an annual basis is for the most part a developed, highly-populated region. Reporting may be positively biased towards these areas, which not only have higher human population densities, but also coastlines that facilitate easy shoreline access (e.g., sandy beaches) and are heavily used by the public. In comparison, many of the coastal areas in the northern Virginia region of the bay have historically documented lower numbers of strandings. These regions are typically less inhabited and comprised largely of undeveloped land or infrequently visited vacation and weekend homes. Therefore, stranding datasets may not accurately represent total mortality occurring within Virginia's waters. Due to these issues, I have largely excluded strandings from the northern bay from our analyses, but if observation effort data were available to correct stranding datasets for observer bias, then these data could be used more productively. Beach monitoring has found to be very effective in increasing stranding documentation of marine animals (Lopes-Souza et al. 2015), although is often difficult to implement due to high labor and cost demands.

Additionally, documentation of stranding events rely not only on discovery by a member of the public, but also the observer's knowledge and action in reporting it. Although many people may know sea turtles are threatened and endangered species, members of the general public are not necessarily aware of the stranding network and who to call to report a stranding in a timely manner. The Virginia Aquarium & Marine Science Center Foundation Stranding Response Program (VAQS) has been responding to marine mammal and sea turtle strandings within Virginia since 1987 (Swingle et al. 2016). The efforts of VAQS are likely well known throughout southeast Virginia, but locals from regions in isolated parts around the bay, as well as summer vacationers to the

area, may not be familiar with reporting procedures. The knowledge of beachgoers likely plays an important role in the number of reported strandings (Huggins et al. 2015), and educational campaigns have been found effective in increasing overall reporting rates of stranded animals (Batista et al. 2012). The distribution of informative flyers is a relatively inexpensive method that can be implemented in areas with historically low reporting rates to increase awareness of VAQS reporting efforts. Such actions may increase the spatial coverage of documented strandings throughout the state and help decrease reporter bias, yielding a more complete stranding dataset and allowing for a more accurate understanding of the distribution of Virginia's sea turtles.

A recently implemented program by VAQS further highlights the potential that educational campaigns and outreach efforts have in improving reporting coverage and contribute to curbing turtle mortality in this region. The Virginia Aquarium & Marine Science Center Stranding Response Team's Pier Partners (<https://www.virginiaaquarium.com/conservation/pier-partners>) began as a pilot program in 2014 to better manage the large number of turtles incidentally caught by pier fishermen each year. Through increased outreach and educating local fishermen on proper sea turtle handling techniques, the program has been very successful in increasing the recovery and rehabilitation of hooked sea turtles. Continued growth and development of this program throughout other areas of the bay can help increase public awareness and improve recreational fishing knowledge of sea turtle entanglement. Furthermore, such programs instructing local fishermen on proper handling techniques if faced with a turtle entanglement can be very beneficial in both the recreational and commercial environment. If confronted with a sea turtle entanglement, it is possible that fishermen

may be hesitant to report the event due to fear of negative repercussions on the fishing industry. Therefore, providing the educational tools to instruct fishermen on how to safely remove entangled turtles may encourage them to take appropriate actions to increase the likelihood that an entrapped turtle is released alive and with minimal injuries. Such actions may reduce the frequency of lethal human-turtle interactions and decrease the number of mortality events occurring in Virginia's waters.

Despite caveats that must be considered when interpreting stranding data, information from several years of validated stranding records are extremely informative for evaluating potential trends in drivers of mortality. With relatively simple requirements for the drift simulation model developed in this thesis, including stranding records and ocean circulation models, there is great potential to apply this methodology to strandings around the globe. 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 model could easily be applied to strandings in other geographic regions. In addition to sea turtles strandings, this model also has potential to be used to better understand mortality locations of stranded marine mammals or sea birds. The ability to use stranding data to determine likely locations of mortality for marine megafauna is an invaluable tool that can provide significant information to inform the development of effective management measures.

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VITA

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Bianca Silva Santos was born in Raritan, NJ on November 28, 1991. She graduated from Bridgewater-Raritan High School in Bridgewater, NJ in 2010 and went on to earn a B.S. in Marine Vertebrate Biology and a minor in Ecosystems and Human Impacts from Stony Brook University in Stony Brook, NY. During her undergraduate career, Bianca spent two years as an undergraduate research assistant with Stony Brook's Marine Animal Disease Laboratory, where she pursued an honors thesis on parasitic success in oysters. She also completed a Research Experience for Undergraduates program with the University of Washington and spent a summer studying salmon growth in Alaska.

Bianca graduated *magna cum laude* and with School of Marine and Atmospheric Sciences departmental honors from Stony Brook University in May 2014. In August 2014, she entered the graduate program at the Virginia Institute of Marine Science, College of William and Mary, in Gloucester Point, VA, under the advising of Dr. David Kaplan. She earned her M.S. in Marine Science with a sub-concentration in marine policy in August 2017 and was selected as a NOAA Sea Grant Knauss Fellow for 2018-2019.