## Research Article



# Characterizing Watercraft-Related Mortality of Sea Turtles in Florida

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ABSTRACT Mortality from being struck by a motorized watercraft is considerable for many aquatic vertebrates around the world, including sea turtles. We studied stranded (i.e., dead, sick, or injured) sea turtles found in Florida, USA, during 1986-2014 and identified those with sharp force or blunt force injuries indicative of a vessel strike. About a third of stranded loggerheads (Caretta caretta), green turtles (Chelonia mydas), and leatherbacks (Dermochelys coriacea) had a vessel-strike injury (VSI). The frequency of this injury was lower but still substantial for stranded Kemp's ridleys (Lepidochelys kempii; 26.1%) and hawksbills (Eretmochelys imbricata; 14.8%). Over the study period, the annual number of stranded loggerheads, green turtles, and Kemp's ridleys with a VSI increased as did the annual number of vessels registered in Florida. Eighty-one percent of the stranded turtles with a VSI were found in the southern half of Florida and 66% of those were found along the southeast coast. By coastal county, the proportion of stranded sea turtles with a VSI was positively related to the mean annual number of registered vessels. The percentage occurrence of a VSI was highest for adult loggerheads, green turtles, and leatherbacks, and reproductively active individuals appeared to be particularly vulnerable to these injuries. We conducted necropsies on 194 stranded sea turtles with a VSI and concluded that this injury was the cause of death or the probable cause of death in  $\geq$  92.8% of these cases. During 2000–2014, we estimate that the mean annual numbers of stranded sea turtles that died from a VSI were 142-229 loggerheads, 101-162 green turtles, 16-32 Kemp's ridleys, 4–6 leatherbacks, and 2–4 hawksbills. Considering that only about 10–20% of sea turtles that died likely washed ashore, the overall annual mortality may have been 5-10 times greater than that represented by strandings. Most of the significant clusters of stranded sea turtles with a VSI occurred at inlets or passes and the probability that a stranded sea turtle had a VSI decreased with increasing distance from inlets or passes, navigable waterways, and marinas. We suggest focusing initial management efforts on reducing watercraft-related mortality for all sea turtle species around 8 inlets in southeast Florida, reproductively active loggerheads and green turtles along the coast of southeast Florida, and Kemp's ridleys and adult male loggerheads at passes along the coast of southwest Florida. Published 2019. This article is a U.S. Government work and is in the public domain in the USA. The Journal of Wildlife Management published by Wiley Periodicals, Inc. on behalf of The Wildlife Society.

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The use and reach of motorized watercraft have increased rapidly since 1950 (Davenport and Davenport 2006).

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<sup>2</sup>Present address: NOAA Fisheries, Office of Protected Resources, 7600 Sand Point Way, Seattle, WA 98115, USA. Unfortunately, these vessels pose a serious threat to wildlife. They strike and kill aquatic vertebrates in freshwater (Killgore et al. 2011, Heinrich et al. 2012), estuaries (Burger and Garber 1995, Laist and Shaw 2006), and marine environments (Van Waerebeek et al. 2007, Ramírez-Macías et al. 2012). When sustaining injuries from motorized watercraft, animals are struck by the hull or by some portion of the steering or propulsion system (Rommel et al. 2007). The most commonly recognized injuries are parallel linear or curvilinear wounds made by spinning propellers.

All air-breathing aquatic vertebrates are at risk from being struck by motorized watercraft, which is a prominent mortality factor for cetaceans (Laist et al. 2001, Van Waerebeek et al. 2007), sirenians (Maitland et al. 2006, Runge et al. 2007), pinnipeds (Bexton et al. 2012, Denkinger et al. 2015), sea otters (Enhydra lutris nereis; Kreuder et al. 2003), crocodilians (Grant and Lewis 2010), and turtles (Heinrich et al. 2012, Denkinger et al. 2013). Many large fishes that feed near the surface have been documented with scars from a vessel-strike injury (VSI) including whale sharks (Rhincodon typus; Speed et al. 2008, Ramírez-Macías et al. 2012), manta rays and devil rays (Mobulidae; Couturier et al. 2012), basking sharks (Cetorhinus maximus; Kelly et al. 2004), and ocean sunfish (Mola mola; Porcasi and Andrews 2001). The Atlantic sturgeon (Acipenser oxyrinchus oxyrinchus) spends most of its time near the bottom but lives in shallow areas and is also prone to vessel strikes (Balazik et al. 2012). The propellers of vessels kill small fishes (Killgore et al. 2011) and larval fishes (Killgore et al. 2001), and this could represent a substantial mortality that is not well documented (Whitfield and Becker 2014).

Mortality from motorized watercraft is of concern in Florida for several species with heightened conservation status. Vessel strikes are a major cause of mortality and injury to right whales (*Eubalaena glacialis*; Kraus 1990, Knowlton and Kraus 2001, van der Hoop et al. 2013). About 25% of the known deaths of threatened Florida manatees (*Trichechus manatus latirostris*) during 1979–2004 resulted from a VSI, making this the most common anthropogenic cause of death for manatees (Rommel et al. 2007). Heinrich et al. (2012) determined that 10.4% of the Suwannee cooters (*Pseudemys concinna suwanniensis* [species of special concern in FL]) collected during the early 2000s from rivers of west-central Florida had evidence of a healed VSI and suspected the mortality rate from this source was even higher.

Five species of sea turtles regularly occur in Florida. These include the threatened loggerhead (*Caretta caretta*) and green turtle (*Chelonia mydas*), and the endangered Kemp's ridley (*Lepidochelys kempii*), leatherback (*Dermochelys coriacea*), and hawksbill (*Eretmochelys imbricata*). The federal recovery plan for each identifies watercraft-related mortality as a threat. The most recently revised recovery plan for the loggerhead (National Marine Fisheries Service and U.S. Fish and Wildlife Service [USFWS] 2008) lists minimizing watercraft-related mortality as a recovery objective and categorizes developing and implementing a strategy to reduce interactions with these vessels as one of the highest priority recovery actions.

A detailed characterization of watercraft-related mortality is needed to inform assessments of the populationlevel effects of this threat and to effectively prioritize, develop, and target any conservation strategies aimed at reducing it. The objective of our descriptive study was to determine the magnitude and spatiotemporal characteristics of watercraft-related mortality of sea turtles in Florida and how it varies by species and life stage using data collected on stranded (i.e., dead, sick, or injured) sea turtles.

# **STUDY AREA**

We used data collected during 1986–2014 from stranded sea turtles found along shorelines or floating in marine or estuarine waters of the 35 coastal counties in Florida, USA (Fig. 1). These counties have an overall shoreline length of 13,576 km (including offshore islands, sounds, bays, rivers, and creeks to the head of the tidewater or to a point where tidal waters narrow to a width of 30.5 m (https://coast.noaa.gov/data/docs/states/shorelines.pdf, accessed 14 Feb 2019).

Five species of sea turtles are regularly documented as strandings in Florida (loggerheads, green turtles, Kemp's ridleys, leatherbacks, and hawksbills) with a sixth species, the olive ridley (Lepidochelys olivacea), being documented only rarely. Stranded sea turtles are usually discovered after washing up along shorelines that are directly adjacent to the Gulf of Mexico or to the Atlantic Ocean (i.e., a coastline; 2,170 km in Florida). Most of the stranded sea turtles are documented on the open, sandy beaches of barrier islands (accounting for about 1,300 km of the coastline). On these beaches, the vegetation closest to the water (but usually above the highest tide line) is typically low-lying pioneer species such as railroad vine (Ipomoea pes-caprae) or coastal searocket (Cakile lanceolata) with grasses such as seaoats (Uniola paniculata) often occurring a little farther up on the beach. Recreational use of these beaches is common yearround and most have either adjacent or nearby real estate development. The southernmost coastline in Florida (about 200 km from the southern half of Miami-Dade County



Figure 1. Coastal counties in Florida, USA, where stranded (i.e., dead, sick, or injured) sea turtles were found along shorelines or floating in marine or estuarine waters, 1986–2014. Stranded sea turtles included loggerheads, green turtles, Kemp's ridleys, leatherbacks, and hawksbills.

through most of southern Monroe County) is a coral cay archipelago (the Florida Keys). Many of these islands have narrow sandy beaches but many also are ringed to some extent by red mangrove (*Rhizophora mangle*) or black mangrove (*Avicennia germinans*). These islands also tend to have a relatively high degree of real estate development.

There are 2 portions of Florida's coastline along the Gulf of Mexico where relatively few stranded sea turtles are documented. This is likely because there is little sandy beach and these coastlines are largely remote and undeveloped. The first is about 350 km of coastal salt marshes from Wakulla County through Pasco County. This shoreline is dominated by needlerush (*Juncus roemerianus*) and smooth cordgrass (*Spartina alterniflora*). The second is about 200 km of shoreline from southern Collier County through northern Monroe County. This shoreline is within the Ten Thousand Islands National Wildlife Refuge and Everglades National Park and is dominated by red and black mangrove.

The climate of most of Florida is humid subtropical with 4 seasons (winter, spring, summer, and fall). The climate of the southern tip of Florida (from West Palm Beach County through Monroe County) is tropical with 2 predominant seasons (winter and summer). The rainy season in Florida is typically from late spring through early fall (May–Oct).

## **METHODS**

### Stranding Data and Trends

Participants in the Florida Sea Turtle Stranding and Salvage Network (STSSN) collected and reported data on stranded sea turtles found in Florida during 1986-2014 using standardized protocols described in Foley et al. (2005). This work was conducted under the authorization of an Endangered Species Act Section 6 cooperative agreement between the USFWS and the Florida Fish and Wildlife Conservation Commission. There were no dedicated surveys to locate stranded sea turtles (including those that were still floating), but there were daily surveys for signs of sea turtle nesting on the sandy beaches along Florida's coastline primarily from April through September (Witherington et al. 2009). Personnel who conducted these surveys (typically participants in the STSSN) also documented or reported any stranded sea turtles that were encountered. Otherwise, reports from the public triggered most of the response that resulted in the documentation of stranded sea turtles.

We identified stranded sea turtles with a definitive VSI by  $\geq 1$  linear or curvilinear sharp force injuries created by an edged object such as a propeller or a sharp skeg. We describe these wounds as chop wounds based on features that include skin incision with a deep groove or comminuted fractures of the underlying bone (DiMaio and DiMaio 2001). We additionally identified stranded sea turtles with a probable blunt force VSI created by a hull or by a rounded feature of the steering or propulsion system. These blunt force injuries typically involved large or discrete areas of the body, usually depressing the fractured bone (i.e., crushing a portion of the body), lacerating the skin, and exposing

organs or soft tissue. We considered the latter injuries as a probable VSI because there were other possible causes such as strikes by a dredge or a malicious human action (e.g., delivering a blow with a club).

We classified the condition of stranded sea turtles found dead by their degree of decomposition. Mildly decomposed carcasses may have had rigor mortis, but the eyes were clear and there was no smell of decomposition or evidence of bloating. Moderately decomposed carcasses had a mild to moderate smell of decomposition with mild to moderate bloating and bulging eyes. In this case, the superficial (keratinized) layers of the skin may have started to detach. Severely decomposed carcasses had a foul smell and were severely bloated or were a mass of rotting flesh if already degassed. Layers of the skin of these carcasses were detaching or missing, and bony structures may have been disarticulating.

We used the curved carapace length (CCL; measured from the nuchal notch to the posterior marginal tip) to group stranded sea turtles by size. We chose this measurement over the straight-line carapace length (SCL) because the CCL was more commonly determined than the SCL (taken 91.4% vs. 51.1% of the time, respectively, when a turtle was measured). We considered a stranded sea turtle to be an adult male if it had a tail described as extending well beyond the carapace. This usually meant that the tail extended  $\geq 20$  cm beyond the posterior margin of the carapace, but observers did not always take tail measurements. We assumed a sea turtle was an adult female if it had a tail that did not extend beyond the carapace and its size was equal to or greater than that typical of nesting females (CCL  $\geq$ 145 cm for leatherbacks [Stewart et al. 2007],  $CCL \ge 101.1$  cm for green turtles [National Marine Fisheries Service and USFWS 1991], CCL ≥98.6 cm for loggerheads [Turtle Expert Working Group 2009], CCL ≥84.0 cm for hawksbills [Bjorndal et al. 1985], and CCL ≥63.5 cm for Kemp's ridleys [Turtle Expert Working Group 2000]). Regardless of carapace length, we also recognized adult female sea turtles by the presence of shelled eggs (visible during necropsy or because of injuries) or by flipper tags applied previously when the turtle had emerged to nest. Lastly, we assumed sea turtles at a size equal to or greater than that typical of nesting females were adults of unknown sex when their tail was missing or not described.

We estimated trends in the annual number and proportion of stranded sea turtles with a VSI during 1986-2014 using the statistical software R version 2.5.0 (R Core Team 2014). We modeled these as a function of time (year) using negative binomial regression for numbers and logistic regression for proportions. For each of the 3 most common species (loggerheads, green turtles, and Kemp's ridleys), we fit 4 negative binomial regression models and 4 logistic regression models. Three of each of these models included time as either a linear, quadratic, or cubic covariate, and the fourth was an intercept-only model. We assessed the relative support for each model using Akaike's Information Criterion (Akaike 1973) with a small-sample bias adjustment (AIC; Burnham and Anderson 2002). In each case, we considered the model with the lowest AIC<sub>c</sub> to be the best-approximating model and based all inferences on that model.

To generally characterize any likely changes in the numbers of vessels operating in Florida during the study period, we obtained data on annual vessel registrations from the Florida Department of Highway Safety and Motor Vehicles. With these data, we fit an additional set of 4 logistic regression models to relate the proportion of stranded sea turtles with a definitive VSI (all species combined) to the mean annual number of vessel registrations by coastal county during 2000-2014. For these models, we considered the counties from Pasco County to Wakulla County (an 8-county stretch; Fig. 1) as a single county because of low stranding numbers (these counties combined had <1% of all stranded sea turtles). Three of these models included the annual number of vessel registrations as either a linear, quadratic, or cubic covariate, and the fourth was an intercept-only model. As before, inference was based on the best-approximating model as determined by the lowest AIC.

## Necropsies

A board-certified veterinary pathologist (B. A. Stacy) performed a necropsy on a subset of stranded sea turtles with a VSI. The objectives of the necropsies were to determine if injuries were antemortem or postmortem for those turtles found dead, to evaluate the VSI as the potential cause of death, and to assess the general health of the turtles immediately prior to incurring the VSI. We took samples of wound margins and other tissues for histopathology if they were likely to yield additional information relevant to determining if the turtle was alive at the time of sustaining the VSI or to identifying disease.

We diagnosed wounds as antemortem if we observed any of the following signs of vitality: hemorrhage, severe blood loss, inflammation, or wound healing (e.g., re-epithelialization, fibroplasia, remodeling of bone). We detected severe blood loss (hypovolemic anemia) by the absence of blood within the heart or by the presence of thin, watery blood, typically in combination with prominent pallor of visceral organs. We did not conclude that there was evidence of blood loss if other conditions potentially associated with severe anemia were present, such as diminished nutritional condition or inflammatory disease. We examined wound margins histologically when poor carcass condition resulting from decomposition, damage by scavengers, or prolonged immersion in water may have obscured signs of vitality at the time of injury or when death may have quickly followed injury (i.e., when inflammation and healing responses would not have had time to become grossly visible). During these wound margin examinations, we looked for infiltration of the wound by leukocytes or for discoid and segmental myofiber disintegration indicative of contractile potential at the time of injury (Stacy et al. 2014). Because the contractile potential of muscle usually remains for at least several hours after death (i.e., a supravital feature), this finding would only allow us to categorize the timing of a VSI in the latter case as perimortem. We identified postmortem injuries by an absence of vital or supravital features. We considered the timing of a VSI to be unknown if we could not find any evidence of vitality and if we could not evaluate wound margins histologically.

We concluded that a VSI was the cause of death (COD) when it was antemortem and resulted in damage to any vital organs or structures. This determination was based on the presence of critical (i.e., clearly fatal) wound features, such as those that compromised neurological or cardiopulmonary function by damage to the brain, cervical spinal cord, heart or major vessels, or lungs, or resulted in exsanguination, severe infection, or aspiration (i.e., drowning). We also considered severe or complicating conditions in our COD determinations, specifically wound features that may not have been immediately fatal by themselves but that would worsen the condition of an injured turtle to the extent that they likely caused or contributed to the death. These severe wound features included trauma involving the liver, gastrointestinal tract, or kidneys, transection of the carapacial spinal cord, or exposure of the coelomic cavity. We designated a VSI as the probable COD if it was antemortem and was likely to have impaired vital function or if it was perimortem and affected vital organs or structures. We concluded that a VSI was not the COD if it caused no apparent fatal injuries or complications, or if it was postmortem. For carcasses in which vital organs and structures were missing or incomplete because of decomposition or scavenging, we evaluated the likelihood that a VSI was the COD based on the location and depth of the injuries.

For each species, we estimated the mean annual minimum number of sea turtles that died from a VSI in Florida during 2000–2014 by first multiplying the mean annual number of stranded sea turtles (of that species) with a definitive VSI by the percentage of all necropsied turtles for which the VSI was the COD. Assuming stranding probabilities of 10–20% (derived from Epperly et al. 1996, Hart et al. 2006), we then multiplied this number by 5 (using a stranding probability of 20%). We estimated the mean annual maximum number of sea turtles that died from a VSI in Florida during 2000–2014 by first multiplying the mean annual number of stranded sea turtles (of that species) with a definitive or probable VSI by the percentage of all necropsied turtles for which the VSI was the COD or the probable COD. We then multiplied this number by 10 (using a stranding probability of 10%).

We assessed necropsied sea turtles to identify predisposing health factors that may have increased the likelihood of being struck by a vessel. We considered nutritional condition, contents of the digestive tract, previous injuries, amount and type of epibiota, and any disease processes regarded as being clinically significant. For each turtle, we also evaluated the possibility that it had been suffering from brevetoxicosis (from exposure to a harmful algal bloom [*Karenia brevis*]). We concluded the latter to be likely if the necropsied turtle had a concentration of brevetoxin in a sample of the liver, kidney, lung, or contents of the digestive tract that was above baseline concentrations (Foley et al. 2019), or if the turtle was found coincident with an unusually high number of stranded sea turtles during a *K. brevis* bloom.

## **Spatial Analyses**

We produced a map of the locations of stranded sea turtles in Florida (http://geodata.myfwc.com/datasets/sea-turtlestrandings-florida) and generated 1-km-diameter hexagonal cells over the extent of these records. To each hexagonal cell, we assigned a count of stranded sea turtles with and without a definitive VSI by species. We then identified significant clusters (P < 0.05) of stranded turtles with a definitive VSI based on the Local Moran's I statistic (Anselin 1995), calculated using ArcGIS (Environmental Systems Research Institute, Redlands CA). We defined the spatial relationship among hexagonal cells using a queen-contiguity spatial weights matrix. For this analysis of spatial clusters, we considered only cells within which  $\geq 1$  stranded sea turtle was found (5,655 cells).

We used a mixed-effects logistic regression model to evaluate the influence of inlets or passes, navigable waterways, and marinas on the probability that a stranded sea turtle had a definitive VSI. The response variable was binary and represented the VSI status (1 = definitive VSI present,0 =definitive VSI not present) of each stranded sea turtle. For this analysis, we included all hexagonal cells with  $\geq 1$ stranded turtle that was  $\leq 1.5$  km from a shoreline (4,780 cells). Our rationale for omitting cells >1.5 km from shore was to focus our analysis where the majority (97%) of stranded sea turtles were found. We used a logit link function to model the binary response as a linear combination of 3 covariates: distance (in km) from each cell to the nearest inlet or pass, navigable waterway, and marina. We obtained location data on the geographic features of interest from the Florida Fish and Wildlife Conservation Commission's geographic information system (GIS) data repository. We compiled inlet and pass locations by combining 2 data sets in the repository (http://ocean. floridamarine.org/arcgis/rest/services/Oil\_Spill/ACPGRP/ MapServer/9 and http://atoll.floridamarine.org/arcgis/rest/ services/FWC\_GIS/OpenData\_Boating/MapServer/4). We used navigable waterways that were digitized from National Oceanic and Atmospheric Administration (NOAA) Nautical Charts (http://atoll.floridamarine.org/ arcgis/rest/services/FWC\_GIS/OpenData\_Boating/ MapServer/11). A statewide boating access facilities in-

ventory and economic study produced data on the locations of marinas (http://atoll.floridamarine.org/arcgis/rest/ services/FWC\_GIS/OpenData\_Boating/MapServer/1).

To facilitate model-fitting, we standardized all continuous predictor variables with a mean of zero and a standard deviation of 1. Additionally, to account for spatial autocorrelation among observations due to multiple observations of stranded turtles in the same hexagonal cell, we included HEXID (a unique hexagonal cell identifier) as a random effect associated with the model intercept (Gelman and Hill 2007). We fit the mixed-effects logistic regression model using the statistical software R version 2.5.0 (R Core Team 2014) and the generalized linear mixed models (Template Model Builder) function from the package GLMMTMB (Brooks et al. 2017). We assessed goodness of fit by conducting the le Cessie-van Houwelingen-Copas-Hosmer goodness-of-fit test, as implemented in the R package RMS (Harrell 2018). Lastly, we assessed the classification accuracy of the fit model using an area under the curve (AUC) statistic, as implemented in the R package ROCR (Sing et al. 2005), where AUC ranged from 0 to 1, and where higher AUC values indicated greater classification accuracy.

# RESULTS

## Stranding Data and Trends

During 1986–2014, 10,962 stranded sea turtles documented in Florida had a definitive or probable VSI, accounting for 31% of all strandings (Table 1). Most (87%) of the stranded sea turtles were found washed ashore. Of those found floating, 77% were  $\leq 1.5$  km from a shore (i.e., only 3% of all stranded sea turtles were documented floating >1.5 km from a shore). About 12% of stranded sea turtles with a definitive VSI (n = 954) were alive when found, but only 1.7% (n = 124) were successfully rehabilitated and then released.

The annual number of stranded loggerheads, green turtles, and Kemp's ridleys with a definitive VSI, and the annual proportion of stranded loggerheads and Kemp's ridleys with these injuries increased during 1986–2014 (Fig. 2). Over this same period, the number of vessels registered in Florida each year increased by about 50% (Fig. 3A). There were typically <10 stranded leatherbacks and hawksbills with a definitive VSI found each year, and there were no overall increases or decreases in those numbers during the study period.

About 85% of stranded sea turtles with a definitive VSI were found in the southern half of Florida (55% in the southeast and 30% in the southwest; Fig. 1). The proportion of stranded sea turtles with a definitive VSI was greatest in 4 contiguous counties along the southeast coast (0.39–0.45 by county for Martin County to Miami-Dade County; Fig. 1). By coastal county during 2000–2014, the proportion of stranded sea turtles with a definitive VSI was positively related to the mean annual number of vessel registrations (Fig. 3B).

Stranded loggerheads, green turtles, Kemp's ridleys, and hawksbills with a definitive VSI were found most often during March–August (75.9%, 61.1%, 66.4%, and 75.4%, respectively). Stranded leatherbacks with a definitive VSI were found primarily during November–May (81.2%) with

**Table 1.** Number of stranded sea turtles documented by species and number and percentage with a vessel-strike injury (VSI) in Florida, USA, 1986–2014. A definitive VSI (DVSI) was  $\geq 1$  linear or curvilinear chop wounds. A probable VSI (PVSI) was a blunt force injury resulting in fractures.

Species	Number	Number with a DVSI	Number with a DVSI or a PVSI	% with a DVSI	% with a DVSI or a PVSI
Loggerhead	19,111	4,217	5,983	22.1	31.3
Green turtle	11,631	2,763	3,758	23.8	32.3
Kemp's ridley	2,738	413	714	15.1	26.1
Leatherback	620	133	213	21.5	34.4
Hawksbill	635	57	94	9.0	14.8
Olive ridley	4	0	0	0.0	0.0
Unknown	1,067	108	200	10.1	18.7
Total	35,806	7,691	10,962	21.5	30.6



Figure 2. Numbers and proportions of stranded loggerheads, green turtles, and Kemp's ridleys with a definitive vessel-strike injury (VSI) each year in Florida, USA, 1986–2014. A definitive VSI was  $\geq 1$  linear or curvilinear chop wounds. We estimated trends using the best-approximating negative binomial regression model (for numbers) or logistic regression model (for proportions), which included either a quadratic or cubic relationship with time, depending on species. On each graph, we show the estimated relationship based on the best-approximating regression model and include the 95% confidence intervals. All trends increased over time except for the proportion of stranded green turtles with a VSI.

almost half found during March–May (45.9%). By species, the proportion of stranded sea turtles with a definitive VSI generally tended to increase with increasing size although there also tended to be a peak at about the middle point of the size range (Fig. 4). Eighteen of the stranded leatherbacks that were measured were <100 cm CCL and none had a VSI. Otherwise, the proportion of stranded leatherbacks with a definitive VSI for size classes  $\geq$ 100 cm CCL (by 20-cm increments, excluding adults) was always around 20%. Stranded adult Kemp's ridleys and hawksbills had a relatively low percentage occurrence of a definitive VSI, but for stranded loggerheads, green turtles, and leatherbacks, the percentage occurrence of a definitive VSI was greatest for adults (including both sexes; Table 2). The locations and timing of stranded adult loggerheads and green turtles with a VSI largely corresponded to areas of major nesting beaches during the mating and nesting seasons (Fig. 5).

#### Necropsies

We necropsied 194 stranded sea turtles with a VSI, including 153 found dead and 41 found alive but that



**Figure 3.** Number of vessels registered in Florida, USA, each year, 1986–2014 (A), and the proportion of stranded sea turtles (including loggerheads, green turtles, Kemp's ridleys, leatherbacks, and hawksbills) with a vessel-strike injury (VSI) in relation to the mean annual number of vessels registered by coastal county in Florida during 2000–2014 (B). We obtained data on vessel registrations from the Florida Department of Highway Safety and Motor Vehicles. We combined data on stranded sea turtles and vessel registrations in the area from Pasco County through Wakulla County because of low numbers of stranded sea turtles. We estimated the relationship in the latter graph using the best-approximating logistic regression model that included a cubic relationship between the 2 variables. We show the estimated relationship and include the 95% confidence interval. The proportion of stranded sea turtles with a VSI was positively related to the mean annual number of vessel registrations.

died within 24 hours (no cases of euthanasia). These turtles were found during 2001–2015, but most (179/194, 92.3%) were found during 2009–2014. Six were found during 2015. The necropsied sea turtles included all species (99 green turtles, 46 loggerheads, 46 Kemp's ridleys, 2 leatherbacks, and 1 hawksbill), represented all stages of decomposition (Table 3), were found in all regions (Table 3), and included those with characteristics of a definitive VSI (n = 144) and those with characteristics of a probable VSI (n = 50). In 142 of the necropsied turtles that were discovered dead (142/ 153, 92.8%), we found evidence that the VSI was either antemortem (n = 114) or perimortem (n = 28). We identified antemortem injuries by hemorrhage (27.2%), blood loss (18.4%), acute inflammation (5.3%), chronic inflammation (6.1%), or a combination of inflammation, blood loss, or hemorrhage (43.0%). We identified all perimortem injuries by myofiber disintegration. We could not determine the timing of the VSI in relation to death for the rest of the necropsied turtles (n = 11, 7.2%) because of the degree of decomposition or scavenging. Of these carcasses, 6 were moderately decomposed and 5 were severely decomposed. We detected only 1 postmortem VSI, and this was in a loggerhead that also had an antemortem VSI.

For 180 of the necropsied sea turtles (92.8% of all necropsied turtles, including those found alive), we determined that a VSI was the COD for 146 (75.3%) and the probable COD for 34 (17.5%). For these sea turtles, every VSI that we could evaluate included critical and severe wound features (Table 4). The more critical findings related to the COD included loss of neurological or cardiopulmonary function. Half of the turtles had multiple injuries or complications from injuries involving those systems (e.g., injury to the brain, cervical spinal cord, or lungs with concurrent evidence of blood loss or seawater aspiration; Table 4). Most turtles had injuries involving visceral organs or wound features that exacerbated their condition, including transection of the carapacial spinal cord or exposure of the coelomic cavity. The wound characteristics and their percentage occurrence were similar between turtles for which a VSI was the COD and turtles for which a VSI was the probable COD (Table 4). None of the blunt force wounds examined during necropsies had characteristics typical of strikes by a dredge such as inundation of exposed soft tissues by sediment or excoriation of the skin caused by exposure to dredge slurry. Otherwise, the force required to cause the blunt force injuries we observed was likely only possible through a strike by a motorized watercraft.

Of the 14 cases in which we could not determine the COD, we concluded that the VSI was antemortem in 2 cases and perimortem in 1 case but could not determine the timing of the injury in the remaining cases. All 14 turtles were either moderately or severely decomposed. Complications in assigning a COD included pre-existing conditions such as atrophy of fat or anemia, shark bite wounds that could have been from either scavenging or predation, and exposure to red tide. However, in each case, we regarded the VSI as potentially fatal. Based on our necropsy findings, we estimated the mean annual numbers of sea turtles by species that died from a VSI in Florida during 2000–2014 (Table 5).

We identified pre-existing conditions that may have increased the likelihood of being struck by a motorized watercraft in 46 (23.7%) of the necropsied sea turtles. We observed the following conditions in these turtles (some turtles had >1 condition): high concentration of brevetoxin or not tested for brevetoxin but found during a *Karenia brevis* bloom coincident with an unusually high number of stranded sea turtles (n = 17), severe atrophy of fat of unknown cause (n = 16), intermediate to severe fibropapillomatosis (FP) or FP in conjunction with severe atrophy of fat (n = 8), severe atrophy of fat associated with intense parasitism (n = 3), injury related to fishing gear (n = 3) or shark bites (n = 2), and a previous VSI (n = 1).



Curved carapace length (cm) of stranded sea turtles

**Figure 4.** Proportion of stranded sea turtles with a definitive vessel-strike injury (VSI) by 5-cm size class for 4 species found in Florida, USA, 1986–2014. A definitive VSI was ≥1 linear or curvilinear chop wounds. The size range given for each species ends at typical adult size. The number of stranded sea turtles represented in the graphs by species are as follows: loggerheads (n = 4,119), green turtles (n = 2,417), hawksbills (n = 46), and Kemp's ridleys (n = 338).

#### Spatial Analyses

We created kernel density maps of stranded sea turtles with a definitive VSI for each of the 5 species that regularly occur in Florida (Fig. S1, available online in Supporting Information). For every species, significant clusters of stranded sea turtles with a definitive VSI almost always occurred at an inlet or a pass (Fig. 6). These clusters for multiple species overlapped at thirteen inlets or passes, 8 of which were in southeast Florida (Fig. 6). Parameter estimates from the mixed-effects logistic regression model indicated that the probability of a stranded sea turtle exhibiting a definitive VSI decreased significantly with increasing distance from inlets or passes, navigable waterways, and marinas (Fig. 7; Appendix A). The le Cessie-van Houwelingen-Copas-Hosmer assessment of goodness of fit indicated that the logistic regression model provided an adequate fit to the observed data (Z = -1.48, P = 0.14). Lastly, the AUC statistic of 0.77 indicated that the classification accuracy of the fit model was adequate.

## DISCUSSION

To determine how often a VSI in a stranded sea turtle represented the COD, we first had to determine how often these were antemortem injuries. For some aquatic vertebrates, this can be done easily. The floating carcasses of Atlantic sturgeons (Balazik et al. 2012), Florida manatees (Lightsey et al. 2006), and North Atlantic right whales (Campbell-Malone et al. 2008) tend to float upside down. Therefore, a VSI in the dorsal surface indicates an antemortem occurrence, whereas a VSI in the ventral surface indicates injuries were likely postmortem. But sea turtle carcasses do not usually float upside down and an antemortem VSI involving the ventrum has been repeatedly observed by the authors. Instead, we looked for signs of vitality associated with the wounds to determine if injuries were antemortem or postmortem. However, signs of vitality such as hemorrhage can be washed away, the duration of survival following injury can be too short for the

**Table 2.** Number and percentage of stranded sea turtles with a definitive vessel-strike injury (DVSI) for adults (including by sex when known) and for all others by species in Florida, USA, 1986–2014. A DVSI was  $\geq 1$  linear or curvilinear chop wounds. Some adult turtles were likely included in the all others category because they could not be identified as an adult because of the lack of a carapace measurement.

	Number of stranded sea turtles			% of stranded sea turtles with a DVSI				
Species	All adults	Adult females	Adult males	All others	All adults	Adult females	Adult males	All others
Loggerhead	3,092	879	1,429	16,019	33.2	39.0	33.9	20.0
Green turtle	395	123	166	11,236	48.6	36.6	59.6	22.9
Leatherback	235	32	23	385	26.4	28.1	26.1	18.7
Kemp's ridley	164	49	3	2,574	9.8	6.1	0.0	15.5
Hawksbill	14	3	2	621	7.1	0.0	0.0	9.9



Figure 5. The relative kernel densities (shaded areas) or individual locations (open circles, when a location was >10 km from any other location) of stranded adult loggerheads (A, n = 1,027) or stranded adult green turtles (B, n = 192) with a definitive vessel-strike injury in Florida, USA, 1986–2014. We determined the kernel densities using ArcGIS 10.3 (ESRI, Redlands, CA, USA). The monthly frequency distribution by sex (when known) is also shown. The location and timing of these strandings largely correspond to the major nesting beaches and to the mating and nesting seasons.

development of detectable vital reactions (e.g., inflammation or wound healing), and evidence of wound vitality can be obscured by decomposition or scavenging. In such cases, we relied on detecting myofiber disintegration in wound margins, a supravital reaction that occurs in injured skeletal muscle until contractile potential is lost with the onset of rigor mortis (Stacy et al. 2014). Although we could only conclude that a VSI occurred perimortem based on this finding, it is unlikely that many sea turtles would happen to be struck by a vessel within hours of death from another

**Table 3.** Number and percentage of stranded sea turtles (including loggerheads, green turtles, Kemp's ridleys, leatherbacks, and hawksbills) with a definitive or probable vessel-strike injury (VSI) found in Florida, USA, 1986–2014, and the number and percentage that were necropsied, by condition when found (not including 214 dried carcasses) and by region where found. The necropsied turtles include 6 that were found in 2015. The number of stranded turtles with a VSI included those with a definitive VSI ( $\geq 1$  linear or curvilinear chop wounds) and those with a probable VSI (blunt force injury resulting in fractures). All necropsied sea turtles that were found alive died within 24 hours (no cases of euthanasia) and were in good condition (min. decomposition) at the time of necropsy.

Condition and location of stranded sea turtles with a VSI	Number with a VSI (% of total)	Number with a VSI that were necropsied (% of total)
Condition at stranding		
Alive	1,423 (13.2)	41 (21.1)
Mildly decomposed	1,555 (14.5)	38 (19.6)
Moderately decomposed	4,223 (39.3)	93 (48.0)
Severely decomposed	3,547 (33.0)	22 (11.3)
Region of discovery		
Northeast (Duval-	1,545 (14.1)	23 (11.8)
Volusia)		
Southeast (Brevard-	5,808 (53.0)	71 (36.6)
Miami-Dade)		
Southwest (Pinellas-	3,068 (28.0)	88 (45.4)
Monroe)		
Northwest (Escambia-	541 (4.9)	12 (6.2)
Pasco)		

cause. Furthermore, sea turtles tend to sink when they die and do not float until decomposition generates enough gas within the carcass, which takes up to several days (Koch et al. 2013, Nero et al. 2013). The supravital reactions evident in the stranded turtles of the current study would not occur in these floating carcasses.

Severely decomposed animals were under-represented among the stranded sea turtles we evaluated for wound vitality and it is possible that a postmortem VSI may have been more common in this group than was characterized by our sample. Additional evaluations, however, corroborated that a postmortem VSI is rare even among stranded sea turtles that are found severely decomposed. Necropsies conducted on 17 severely decomposed sea turtles with a definitive or probable VSI found in other southeastern states revealed that these were all either antemortem or perimortem wounds (B. A. Stacy, National Marine Fisheries Service, unpublished data).

Sea turtles can survive being struck by a vessel. Outside of Florida, 2% (Seminoff et al. 2003) to 20% (Denkinger et al. 2013) of the sea turtles found at foraging sites have been documented with scars from a VSI. Similar scars have also been found on 4% of nesting sea turtles (Denkinger et al. 2013). However, even if a sea turtle initially survives a VSI, the injury could cause continuing health issues that may eventually lead to death. In Florida, Norem (2005) determined that 1.9% (49/2,632) of the sea turtles entrained in the intake canal of a coastal power plant had a VSI. In that study, the turtles almost always had a good body condition index (96.1% in a sample of 511) but only 55.1% of those with a VSI did.

A consideration in our characterization of sea turtle mortality associated with a VSI was the influence of a confounding factor. For example, 24% of the necropsied sea turtles had a significant pre-existing health condition. As we defined these, they could have been related to a change in

**Table 4.** Wound features used for cause of death (COD) determination in necropsies of stranded sea turtles with a definitive or probable vessel-strike injury (VSI). These turtles (including 99 green turtles, 46 loggerheads, 46 Kemp's ridleys, 2 leatherbacks, and 1 hawksbill) were found in Florida, USA, 2001–2015. A definitive VSI was  $\geq 1$  linear or curvilinear chop wounds. A probable VSI was a blunt force injury resulting in fractures. Critical features were those that presented an immediate threat to neurological or cardiopulmonary function. Severe features exacerbated the condition of wounded turtles and likely caused or contributed to death in some instances. Variations in the numbers of turtles compared within the categories (columns) were because some turtles could not be evaluated for every wound feature primarily because of state of decomposition and completeness of the carcass.

	COD was VSI		
Wound feature <sup>a</sup>	Found alive	Found dead	COD was probably VSI
Brain injury (C)	10.5% (4/38)	6.7% (7/105)	17.6% (3/17)
Cervical spine injury (C)	2.6% (1/38)	12.4% (13/105)	35.3% (6/17)
Heart or major vessel injury <sup>b</sup> (C)	13.2% (5/38)	11.4% (12/105)	0.0% (0/15)
Open lung wound (C)	31.6% (12/38)	46.6% (48/103)	64.3% (9/14)
Exsanguination (C)	55.3% (21/38)	59.8% (61/102)	
Secondary infection (C)	15.8% (6/38)	12.5% (13/104)	
Aspiration (C)	34.2% (13/38)	28.6% (10/35)	
Multiple critical features	97.4% (37/38)	98.1% (106/108)	85.7% (12/14)
Visceral organ trauma <sup>c</sup> (S)	60.5% (23/38)	55.0% (55/100)	68.4% (13/19)
Carapacial spinal injury (S)	28.9% (11/38)	35.2% (38/108)	44.4% (12/27)
Penetrated coelom (S)	55.3% (21/38)	57.4% (54/94)	77.8% (14/18)
Multiple severe features	86.8% (33/38)	73.8% (79/107)	80.0% (20/25)
Critical and severe features	100% (38/38)	100% (108/108)	100% (27/27)

<sup>a</sup> C = critical; S = severe.

<sup>b</sup> Includes external jugular vein, aorta, or pulmonary or renal arteries.

<sup>c</sup> Includes liver, kidney, or gastrointestinal tract.

behavior, perhaps leading to more time spent at the surface or to a decrease in alertness or mobility, which in turn could have led to an increased likelihood of being struck by a vessel. If the necropsied sea turtles accurately reflect the frequency of such pre-existing conditions among all stranded sea turtles in Florida with a VSI, then a VSI may not be solely responsible for mortality in 24% of these cases. However, 54% of the necropsied sea turtles with preexisting conditions in the present study were diagnosed with brevetoxicosis or FP. The relatively high prevalence of these conditions in our study was likely an artifact of the disproportionately large number of necropsied sea turtles that were from southwest Florida. Brevetoxicosis is almost exclusively limited to Florida's west coast, primarily southwest Florida (Foley et al. 2019), and FP is also most

**Table 5.** Mean annual numbers of stranded sea turtles with a vessel-strike injury (VSI) and estimates of the mean annual mortality due to a VSI by species in Florida, USA, 2000–2014. To determine the likely minimum mean annual mortality (min.), we used only stranded sea turtles with a definitive VSI (DVSI), assumed that 75.3% were killed by this injury, and assumed that these strandings represented 20% of all sea turtles killed by a VSI. To determine the likely maximum mean annual mortality (max.), we used stranded sea turtles with either a definitive or probable VSI (PVSI), assumed that 92.8% were killed by this injury, and assumed that these strandings represented 10% of all sea turtles killed by a VSI. A DVSI was ≥1 linear or curvilinear chop wounds. A PVSI was a blunt force injury resulting in fractures. Stranding probabilities (10–20%) were derived from Epperly et al. (1996) and Hart et al. (2006).

Species	Mean annual number with a DVSI	Mean annual number with a DVSI or a PVSI	Mean annual estimate of mortality (min.–max.)
Loggerhead	189	247	712-2,292
Green turtle	134	175	505-1,624
Kemp's ridley	21	34	79-316
Leatherback	5	7	19-65
Hawksbill	3	4	11-37

common in stranded green turtles from southwest Florida (Foley et al. 2005). For the necropsied sea turtles with a VSI that were not found in southwest Florida, only 16% (17/ 106) had a significant pre-existing health condition. Additionally, sea turtles with these pre-existing conditions may tend to be over-represented in stranding data because many of these conditions are likely to result in positive buoyancy (Schmitt et al. 2013), probably increasing the odds that these carcasses wash ashore.

Of all the cases of a probable VSI that we examined in necropsy, none were determined to have likely been caused by anything other than a motorized watercraft. We think that among stranded sea turtles, most of the blunt force wounds observed are a VSI.

Based on the results of our necropsies, we conclude that a VSI in a stranded sea turtle almost always represents the COD. For stranded sea turtles in Florida with external evidence of a possible COD (~50–60% of the strandings; A. M. Foley, Florida Fish and Wildlife Conservation Commission, unpublished data), a VSI is the most common mortality factor identified for every sea turtle species. Based on stranding numbers, being struck by a vessel causes up to about 30% of the mortality of loggerheads, green turtles, and leatherbacks; up to about 25% of the mortality of Kemp's ridleys; and up to about 15% of the mortality of hawksbills in the nearshore areas of Florida. Overall, we estimate that strikes by motorized watercraft killed a mean of 1,326–4,334 sea turtles each year in Florida during 2000–2014.

Sea turtle mortality due to a VSI has been documented in many areas of the world and typically involves loggerheads or green turtles (Boulon 2000, Hazel and Gyuris 2006, Chaloupka et al. 2008, Casale et al. 2010). Those were also the most common species documented with a VSI in the present study. We additionally documented unprecedented numbers of stranded Kemp's ridleys, leatherbacks, and



**Figure 6.** Locations of significant clusters of stranded sea turtles with a definitive vessel-strike injury (VSI) found in Florida, USA, 1986–2014. A definitive VSI was  $\geq 1$  linear or curvilinear chop wounds. We determined the significant clusters with the Local Moran's I statistic (P < 0.05) individually for 5 species: loggerhead = CC, green turtle = CM, Kemp's ridley = LK, leatherback = DC, and hawksbill = EI. The sea turtle species represented by each cluster is given in parenthesis after the cluster label. If clusters for  $\geq 2$  species coincide, they are represented by 1 location point with all species noted in the label.

hawksbills with a VSI. The percentage occurrence of a VSI among stranded sea turtles in Florida was higher than that documented in most other studies and the numbers of sea turtles (of every species) annually killed in Florida likely exceed those in other areas studied (Boulon 2000, Hazel and Gyuris 2006, Chaloupka et al. 2008, Casale et al. 2010, Denkinger et al. 2013).

The number of stranded loggerheads, green turtles, and Kemp's ridleys with a VSI found each year in Florida increased during our study period. Three potential factors may have contributed to this. The first is the possibility that there may have been some increase in the effort to locate and document stranded sea turtles in Florida during the study period. The Florida STSSN began documenting stranded sea turtles in 1980 and there were initially large increases each year in the extent of Florida's coastal areas covered by the STSSN. However, by 1986 (when the present study was initiated), we consider that the STSSN had achieved (and then maintained) a generally consistent, statewide effort to document stranded sea turtles. Statewide surveys of Florida's sandy beaches for signs of sea turtle nesting began in 1979 and there was an overall increase in the total annual survey length from 222 km in 1979 to 1,331 km in 2014. However, most of this increase occurred during the earliest years (1,020 km surveyed by 1990 and 1,222 km surveyed by 1996).

The increasing annual numbers of stranded turtles with a VSI may also have been due, at least in part, to an increase in the numbers of these species around Florida. Numbers of green turtles and Kemp's ridleys likely increased (Chaloupka et al. 2007, National Marine Fisheries Service et al. 2011), but any positive trend in the number of loggerheads during

much of the study period was not as clear (Turtle Expert Working Group 2009, Witherington et al. 2009).

Lastly, the increasing annual numbers of stranded turtles with a VSI may have been due to an increase in boating activity. Our metric for boating activity was the number of registered vessels, which increased over most of our study period. Our finding that the proportion of stranded sea turtles with a VSI was positively related to the number of vessel registrations indicated that this metric was probably a generally accurate representation of boating activity.

By lifestage, the percentage occurrence of a VSI in stranded sea turtles was greatest for adults of the 3 species that regularly nest in Florida (loggerheads, green turtles, and leatherbacks), and we observed high rates of a VSI for both sexes. Studies of other aquatic turtles have found that adult females (but not adult males) are those most commonly struck by vessels. This has been documented for spiny softshell turtles (Apalone spinifera; Galois and Ouellet 2007), Florida red-bellied cooters (Pseudemys nesloni; Bancroft et al. 1983), common musk turtles (Sternotherus odoratus; Bancroft et al. 1983), map turtles (Graptemys geographica; Bulté et al. 2010), and diamondback terrapins (Malaclemys terrapin; Burger and Garber 1995, Gibbons et al. 2001). This may be due to the relatively large size of these adult females (even compared to adult males), but it may also be a result of their extended movements to reach nesting sites.

Most of the adult loggerheads and green turtles with a VSI were found along the southeast coast of Florida, where the major Florida nesting beaches for both species are located (Witherington et al. 2006a,b). We think that most of these turtles were reproductively active because of the timing of the strandings (primarily spring through early summer;



Figure 7. Estimated relationship between the probability of a stranded sea turtle (including loggerheads, green turtles, Kemp's ridleys, leatherbacks, and hawksbills) exhibiting a definitive vessel-strike injury (VSI) and distance (km) to the nearest inlet or pass (A), to the nearest navigable waterway (B), and to the nearest marina (C) in Florida, USA, 1986–2014. A definitive VSI was  $\geq 1$  linear or curvilinear chop wounds. We derived the predicted probabilities from a mixed-effects logistic regression model. Each regression included all 3 covariates (distances to each geographic feature) where the mean values for the 2 covariates that were not being estimated were applied. The effect of each covariate was significant. The shaded area represents the 95% confidence interval.

Mar–Jul) and because resident adult loggerheads are uncommon along this coast south of Indian River County (Ceriani et al. 2012, 2015; Foley et al. 2014) and resident adult green turtles may be completely absent here (Schroeder et al. 2008). Watercraft-related mortality of breeding adult sea turtles is particularly worrisome because this is the most reproductively valuable lifestage (National Marine Fisheries Service and USFWS 2008).

Foley et al. (2013) identified a loggerhead migratory corridor along the coast of southeast Florida from Brevard County through Monroe County that is used by many reproductively active females. Arendt et al. (2011) documented reproductively active male loggerheads using this same corridor and it is apparent that reproductively active female and male green turtles do too (Schroeder et al. 2008). Additionally, copulating pairs of both species are regularly seen at the surface along this area (A. M. Foley, unpublished data). Female loggerheads and green turtles might be more susceptible to being struck by motorized watercraft when making reproductive migrations because they spend more time near the surface (probably swimming just below the surface, especially during the day) than they do when at resident foraging areas (Hays et al. 1999, Godley et al. 2002, Foley et al. 2013). Migrating males of these species might exhibit similar behavior.

Initial tracking of loggerheads (Arendt et al. 2011, Ceriani et al. 2012, Foley et al. 2013) and green turtles (Schroeder et al. 2008) along the coast of southeast Florida suggested that reproductively active individuals travel relatively close to shore. However, the typical location accuracy at the time of those studies did not allow for a fine-scale assessment of movements. Recent tracking in this area with more finely resolved location data (using global positioning system technology) indicates that reproductively active loggerheads, including females during inter-nesting intervals, spend much of their time <1 km from shore (A. M. Foley, unpublished data; S. A Ceriani, Florida Fish and Wildlife Conservation Commission, unpublished data). This nearshore area could be where many adult loggerheads and green turtles are struck by motorized watercraft.

One conservation approach commonly used to reduce deadly interactions between aquatic animals and motorized watercraft is to educate vessel operators on how to spot these animals, so they can avoid striking them. Unfortunately, signs indicating the presence of sea turtles that could be discerned by vessel operators are infrequent and subtle. Sea turtles generally surface every 10–30 minutes when active and can dive again after only a few seconds (Lutcavage and Lutz 1997). Sea turtles swimming near the surface are also unlikely to produce signs of this activity that are visible above the surface.

Another common approach to reducing the mortality of aquatic animals from motorized watercraft is to establish goslow zones or no-entry areas. To address vessel-strike mortality of right whales, the National Marine Fisheries Service implemented management measures in 2008 to seasonally restrict the speed of vessels  $\geq$  32 m to  $\leq$  18.5 km/ hour in certain areas along the Atlantic coast. An assessment of go-slow zones for reducing mortality of the Florida manatee described the benefits as creating a greater reaction time for avoidance by both the vessel operator and the manatee, and for reducing the severity of injuries if a manatee is struck (Calleson and Frohlich 2007). Go-slow zones could provide the same benefits for sea turtles. Hazel et al. (2007) reported that green turtles reliably avoided motorized watercraft if the vessel speed did not exceed 4 km/hour. After striking hand-built, life-size models of loggerhead carapaces with various motorized watercraft, Work et al. (2010) concluded that decreasing speeds decreased the occurrence of catastrophic injuries. No-entry areas in the eastern United States have been successfully used to keep motorized watercraft away from right whales (Vanderlaan and Taggart 2009) and Florida manatees (King and Heinen 2004) and could also be effective for safeguarding sea turtles. If establishing go-slow zones or noentry areas are not feasible, the fatality rates of a VSI might still be reduced by the increased use of propulsion systems such as jet drives that do not have an exposed propeller or skeg (Work et al. 2010).

We determined that the mortality of sea turtles in Florida from being struck by motorized watercraft is substantial. Efforts to recover these threatened or endangered species will be bolstered by actions that reduce this mortality. Any regulatory actions, such as go-slow zones or no-entry areas, will need to be well justified and efficiently and effectively targeted. To this end, detailed studies of the behaviors and movements of sea turtles and the patterns of motorized watercraft use need to be conducted to determine as precisely as possible when and where sea turtles and motorized watercraft intersect (Shimada et al. 2017).

# MANAGEMENT IMPLICATIONS

In general, geographic features such as inlets or passes, navigable waterways, and marinas (especially in southern

FL) could be high-value targets for management efforts aimed at reducing the number of sea turtles that are struck by vessels. For initial management efforts, we identify 3 more specific priorities. The first is to reduce watercraftrelated mortality for all sea turtle species around 8 inlets in southeast Florida (i.e., Port Canaveral, Sebastian Inlet, Fort Pierce Inlet, St. Lucie Inlet, Jupiter Inlet, Lake Worth Inlet, Boca Raton Inlet, Hillsboro Inlet). The second is to reduce watercraft-related mortality of reproductively active loggerheads and green turtles along the coast of southeast Florida, particularly in Brevard County and from the southern half of St. Lucie County through the northern half of Broward County. The third is to reduce the vessel-strike mortality of Kemp's ridleys and adult male loggerheads at passes along the coast of southwest Florida.

Reducing watercraft-related mortality of sea turtles in Florida could begin through voluntary actions promoted by educational campaigns. For example, these campaigns could emphasize the danger to sea turtles posed by motorized watercraft traveling near the major inlets of southeast Florida and urge slow speeds whenever possible in these areas. During the height of the loggerhead and green turtle mating and nesting season (Mar–Jul), boaters operating along the coast of southeast Florida could be encouraged to avoid or minimize traveling <1 km from shore or to otherwise go as slowly as possible when motoring this close to shore. These boaters could also be educated about the presence of copulating pairs of sea turtles at or near the surface, which would probably be easier to spot, and therefore avoid, than individual turtles at or near the surface.

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# SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

## APPENDIX A. PARAMETER ESTIMATES

Parameter estimates, standard errors, and 95% confidence intervals from a mixed-effects logistic regression model relating the probability of a stranded sea turtle exhibiting a definitive vessel-strike injury (VSI) to 3 covariates (distance in km to the nearest inlet or pass, navigable waterway, and marina). A definitive VSI was  $\geq 1$  linear or curvilinear chop wounds. The stranded sea turtles (including loggerheads, green turtles, Kemp's ridleys, leatherbacks, and hawksbills) were found in Florida, USA, 1986–2014. All the covariates were standardized with a mean of zero and a standard deviation of 1; hence, the parameter estimates represent the change in log-odds for every 1 standard deviation increase in the covariate. Standard deviations of the distances of stranded sea turtles from inlets, navigable waterways, and marinas were 8.0 km, 1.4 km, and 3.8 km, respectively. We included HEXID (a unique hexagonal cell identifier) as a random effect associated with the model intercept. The effect of each covariate was significant, as indicated by a confidence interval that did not overlap zero.

			95% CI	
Parameters	Estimate	SE	Lower	Upper
Fixed effects				
Intercept	-1.406	0.023	-1.451	-1.362
Distance (km) to nearest inlet or pass	-0.066	0.025	-0.116	-0.017
Distance (km) to nearest navigable waterway	-0.353	0.031	-0.413	-0.293
Distance (km) to nearest marina	-0.297	0.030	-0.356	-0.238
Random effect				
Intercept (HEXID)	0.549			