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ECOGRAPHY

Research

Predicted distributions and abundances of the sea turtle 'lost years' in the western North Atlantic Ocean

Nathan F. Putman, Erin E. Seney, Phlippe Verley, Donna J. Shaver, Melania C. López-Castro, Melissa Cook, Vicente Guzmán, Beth Brost, Simona A. Ceriani, Raúl de Jesús González Díaz Mirón, Luis Jaime Peña, Miriam Tzeek, Roldán A. Valverde, Cristóbal Cáceres G. Cantón, Lyndsey Howell, Jonathan A. Ravell Ley, Mandy C. Tumlin, Wendy G. Teas, Charles W. Caillouet Jr, Eduardo Cuevas, Benny J. Gallaway, Paul M. Richards and Katherine L. Mansfield

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Oceanic dispersal characterizes the early juvenile life-stages of numerous marine species of conservation concern. This early stage may be a 'critical period' for many species, playing an overriding role in population dynamics. Often, relatively little information is available on their distribution during this period, limiting the effectiveness of efforts to understand environmental and anthropogenic impacts on these species. Here we present a simple model to predict annual variation in the distribution and abundance of oceanic-stage juvenile sea turtles based on species' reproductive output, movement and mortality. We simulated dispersal of 25 cohorts (1993–2017) of oceanic-stage juveniles by tracking the movements of virtual hatchling sea turtles released in a hindcast ocean circulation model. We then used estimates of annual hatchling production from Kemp's ridley *Lepidochelys kempii* (n = 3), green *Chelonia mydas* (n = 8) and loggerhead *Caretta caretta* (n = 5) nesting areas in the northwestern Atlantic (inclusive of the Gulf of Mexico, Caribbean Sea and eastern seaboard of the U.S.) and their stage-specific mortality rates to weight dispersal predictions. The model's predictions indicate spatial heterogeneity in turtle distribution across their marine range, identify locations of increasing turtle abundance (notably along the U.S. coast), and provide

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valuable context for temporal variation in the stranding of young sea turtles across the Gulf of Mexico. Further effort to collect demographic, distribution and behavioral data that refine, complement and extend the utility of this modeling approach for sea turtles and other dispersive marine taxa is warranted. Finally, generating these spatially-explicit predictions of turtle abundance required extensive international collaboration among scientists; our findings indicate that continued conservation of these sea turtle populations and the management of the numerous anthropogenic activities that operate in the northwestern Atlantic Ocean will require similar international coordination.

Keywords: green turtle, Kemp's ridley turtle, loggerhead turtle, movement ecology, ontogenetic shift, stranding

Introduction

The distribution of a species is of fundamental biological importance because it shapes processes ranging from metabolic and growth rates of individuals to speciation of populations (Lomolino et al. 2006). To effectively manage or restore a species, knowing its distribution and how it changes through time is essential (Franklin 2010). Statistical techniques to explain and predict distributions, especially using species distribution models, are frequently used to correlate environmental data with organism occurrence (Elith and Leathwick 2009). Given the widespread use of species distribution models and the large community of practitioners (Rodriguez et al. 2007), the limitations of this approach are well-known. Concerns typically include 1) unreliable predictions when building models with a small number of observations (especially for species with a wide environmental niche or geographic range); 2) the 'static' nature of predicted distributions; and 3) the weak linkages between ecological theory (e.g. mechanisms that drive distribution) and the construction of species distribution models (Hernandez et al. 2006, Elith and Leathwick 2009, Franklin 2010).

Alternative approaches exist that focus on the mechanisms that influence distribution which, at a basic level, results from reproductive output, movement and mortality of individual organisms (Lomolino et al. 2006). Reproductive output and mortality are often considered by incorporating detailed information on physiological processes of individuals (Evans et al. 2015) (e.g. by solving energy and mass-balance equations as a function of the metabolic costs of thermoregulation and activity (Kearney et al. 2010)) and from population-level demographics (e.g. using population-specific rates in reproductive phenology and thermal tolerance (Chapman et al. 2017)). While movement is also considered in mechanistic models (Cabral et al. 2017), it is typically parameterized as some variation on a random walk and accounting for underlying processes is rare (Holyoak et al. 2008, Merow et al. 2011, Petrovskii and Petrovska 2012).

Nonetheless, in many situations, there is sufficient knowledge about the mechanisms that drive organismal movement to make first-order predictions of species distributions and their variability through time. For instance, the directional movement of marine organisms is strongly tied to ocean circulation processes (Harden-Jones 1968, Hays 2017). Freely-available, high-resolution information on ocean circulation at global and regional scales provides one of the key inputs needed to predict marine species distributions (Fossette et al. 2012). While swimming behavior can play a critical role in many ecological processes (Largier 2003), simulated movements based solely on ocean currents provide a valuable 'null hypothesis' to begin investigating the drivers of species distribution (Putman and Naro-Maciel 2013). Predictions of distribution generated from mechanistic movement models are particularly useful for marine species and life-stages that occupy broad expanses of oceanic habitat, where survey data are lacking over large areas of their range (Putman and He 2013). These models can provide context for observations of organismal occurrence and abundance that would otherwise be unavailable (Fraser et al. 2018, Putman et al. 2018, Smith et al. 2018).

Scientists' attempts to gain insight into the oceanic-stage of juvenile sea turtles has driven considerable development and use of movement models to predict species distributions (Hays and Marsh 1997, Blumenthal et al. 2009, Putman et al. 2010a, 2013, 2015, Gaspar et al. 2012, Scott et al. 2012, 2017, Casale and Mariani 2014, Lalire and Gaspar 2019). Sea turtle species are priorities for conservation efforts across the globe and the lack of information on their distributions by life-stage is identified as a serious limitation to our ability to protect them (Hamann et al. 2010, Rees et al. 2016, Wildermann et al. 2018). Sea turtles nest on sandy beaches where conditions are favorable for egg development and nearby oceanic currents facilitate hatchling movement to nursery habitats (Putman 2018a). Depending on the species, turtles spend 1–15 yr in the open sea, a period coined 'the lost years', because observations on their occurrence are sparse (Carr 1987, Avens et al 2013, Mansfield and Putman 2013). After this period of oceanic dispersal, turtles typically recruit to nearshore foraging grounds and then, some years later, return to the vicinity of their natal site to reproduce (Lohmann et al. 2013, Mansfield and Putman 2013). Modeling dispersal of the juveniles' oceanic stage usually involves releasing virtual hatchling turtles offshore of nesting areas and tracking their movement over a period of months to years through an ocean circulation model, which can provide a prediction of the relative distribution of the population over the time simulated (Putman et al. 2013, Scott et al. 2017, Lalire and Gaspar 2019).

Here, we build on the above approach to predict spatiotemporal variation in the distribution of Kemp's ridley *Lepidochelys kempii*, green *Chelonia mydas* and loggerhead *Caretta caretta* oceanic-stage, juvenile sea turtles from populations in the western North Atlantic Ocean (Fig. 1). We generated predictions using simulated dispersal patterns for

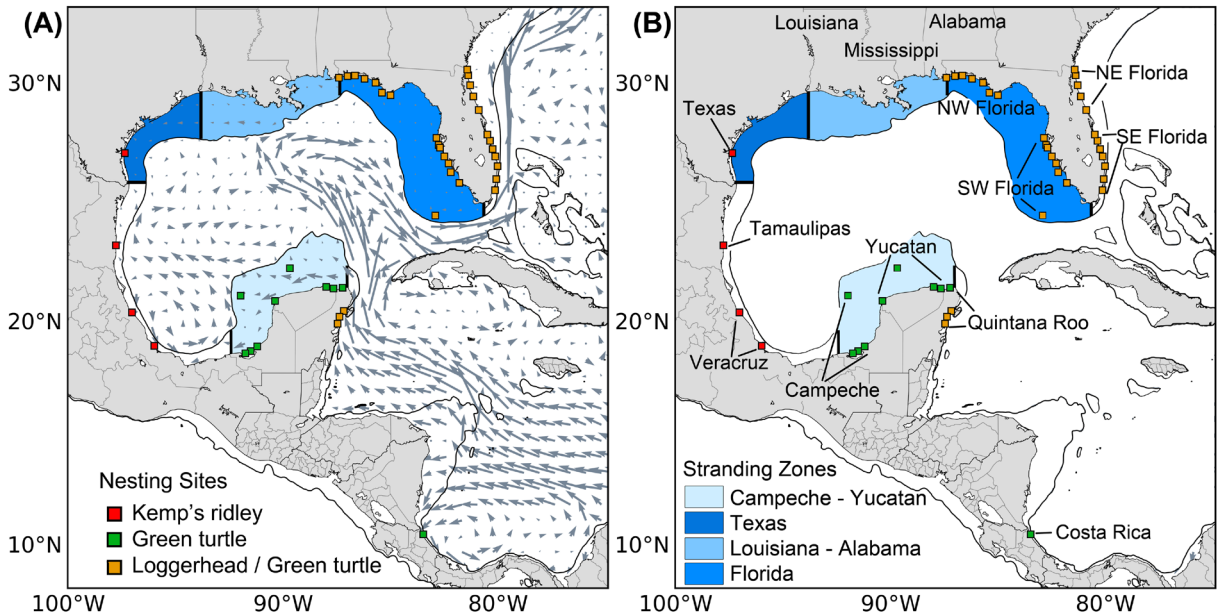

Figure 1. Maps showing the locations of sea turtle nesting sites from which hatchling dispersal was simulated (red squares = Kemp's ridley; green squares = green turtles; orange squares = loggerhead and green turtles). Blue coloration indicates the regions where indices of annual abundance of oceanic-stage turtles generated from dispersal simulations were compared to in situ stranding reports of small turtles (darker shades of blue correspond to areas with higher numbers of stranding records). (A) Shows mean ocean currents from the surface layer of the Global Hybrid Coordinate Ocean Model (HYCOM) in 2015 to provide an indication of dominant circulation patterns influencing the dispersal of young turtles in this region, the thin black line indicates the edge of the continental shelf (200 m isobath). (B) Shows location names used in the text and Supplementary material Appendix 1.

hatchling cohorts from 1993 through 2017 based on Global Hybrid Coordinate Ocean Model (HYCOM) hindcasts (Chassignet et al. 2009). We explicitly accounted for temporal variation in the reproductive output of each species' nesting populations by 1) weighting transport predictions by estimates of annual hatchling production in each nesting region and 2) estimating stage-specific mortality. This allowed us to predict annual spatial variation in the numerical abundance of oceanic-stage sea turtles across the North Atlantic for more than two decades. We then show how these predictions can be used to provide context for available distribution data in young sea turtles that recently recruited to coastal areas by comparing model predictions to long-term datasets on sea turtle strandings across the Gulf of Mexico. We conclude with discussion on the next steps needed to refine these predictions of turtle distributions and the potential for broadening the application of this tool to other situations and marine taxa.

Methods

Focal nesting regions

We examined changes in the distribution and densities of the oceanic-stage of three sea turtle species from 1996 through 2017 from major turtle nesting regions in the western North Atlantic (Kemp's ridley n = 3, green n = 8 and loggerhead n = 5) (Fig. 1, Supplementary material Appendix 1 Table A1, A2). These do not represent all nesting areas but were selected owing to the availability of long-term, consistent monitoring data that allowed us to generate indices of annual hatchling production for the years 1993–2017 (the period that ocean circulation model outputs to simulate dispersal were available). These estimates of hatchling production were used to weight transport predictions from the respective regions. Data on the number of hatchlings released per year were directly available for Kemp's ridley nest sites in Tamaulipas, MX and Texas, U.S. and for green turtle nest sites in Campeche, MX, Yucatan, MX, and the north coast of Quintana Roo, MX. Other regions only had nest counts available, which were converted to hatchling production by using species-specific estimates of eggs produced per nest and clutch survival (Kemp's ridley: 110.0 eggs per nest, 65.0% survival; green: 118.7 eggs per nest, 72.5% survival; loggerhead: 116.8 eggs per nest, 72.0% survival) (Putman et al. 2015).

Kemp's ridley nest counts at Veracruz, MX were only available from 2004 to 2017. To extend this data series we determined the trend in the ratio of Kemp's ridley nesting that occurred in Veracruz relative to Tamaulipas (the ratio of Veracruz to Tamaulipas nests = 0.003 × year − 5.9815; r = 0.63, p = 0.009, n = 14), which was then multiplied by the number of nests recorded in Tamaulipas for the years 1993–2003. Nest counts of green and loggerhead turtles from the east coast of Quintana Roo, MX were unavailable for years 1993–1995. To extend this data record we applied the three year mean of the subsequent three years (i.e. 1996–1998) to each of the missing years.

Dispersal simulations

The movement of young sea turtles during their oceanic stage was simulated using Global HYCOM daily snapshots of surface velocity at 0.08° resolution (Chassignet et al. 2009). HYCOM ocean currents are based on forcing fields and data assimilation that depict ocean conditions at specific times in the past. Dispersal was modeled for years 1993–2017 (HYCOM experiments 19.0, 19.1, 90.9, 91.0, 91.1, 91.2) by ICHTHYOP (ver. 2.2.1) particle-tracking software (Lett et al. 2008). For each nesting region, 350 virtual particles were released daily, just offshore of the primary nesting sites during each of the 60 d of peak hatchling emergence (Fig. 1). This resulted in 21 000 particles released per region annually for 25 turtle cohorts. ICHTHYOP implemented a Runge–Kutta fourth-order time-stepping method whereby particle position was calculated each half-hour as they moved through the HYCOM velocity fields. Virtual particles were tracked for up to 3.5 yr (2.5 yr for Kemp's ridley) to account for the period of the oceanic stage when movement is most dominated by surface currents (Putman et al. 2013, 2015, Naro-Maciel et al. 2017). These drift times are representative of the entire oceanic-stage for Kemp's ridley (~100% of the oceanic stage) and many green turtles (~70–100%). However, loggerheads likely spend considerably more time in the open sea (perhaps 5–15 yr) (Mansfield and Putman 2013, Martins et al. 2018). Thus, the predictions for loggerheads only account for the early portion of the juvenile, oceanic-stage (~23–70%). No swimming behavior was simulated as our aim was to produce a simple model of sea turtle movement and distribution.

The density of oceanic-stage sea turtles was determined for the years 1996 through 2017, as 1996 is the first year when all modeled age classes were represented, i.e. virtual turtles hatched in 1993 (3.5 yr old), 1994 (2.5 yr old), 1995 (1.5 yr old) and 1996 (0.5 yr old). We recorded the percentage of particles within 1 × 1° bins across the North Atlantic for turtles aged 0.5, 1.5, 2.5 and 3.5 yr from each nesting region. For each age class, we multiplied the percentage of particles by the estimate of hatchlings produced at a given nesting region. We then multiplied this value by a daily estimate of oceanic survival based on the median annual estimate (i.e. 81.7%) obtained from the literature by Putman et al. (2015). For each species, these values were summed by age class and nesting region to generate an estimate of turtle abundance in each bin, for each available year. To examine spatial and temporal variability in oceanic-stage turtle distributions we computed the mean density of simulated turtles, the standard deviation of the mean and the slope of correlation between annual density and year (i.e. the trend).

Comparison to strandings data

Data on the spatiotemporal distribution of oceanic-stage, juvenile sea turtles are notoriously difficult to obtain (Carr 1987). After departing the nesting beach as ~5 cm long hatchlings, Kemp's ridley and green turtles typically go unobserved until they return to coastal waters at a size of ~30 cm (Reich et al. 2007, Goshe et al. 2010, Metz and Landry 2016), whereas loggerheads may not revisit coastal areas until ~50 cm (Mansfield et al. 2009, Martins et al. 2018). Aerial surveys flown by the National Marine Fisheries Service, for instance, cannot identify turtles less than ~40 cm carapace length (i.e. the size of oceanic-stage turtles and those that have recently recruited to coastal waters) (Garrison 2015). As a first step toward examining the utility of this model, we compared predicted abundance to a long-term timeseries of sea turtle strandings in the coastal regions of the Gulf of Mexico. Strandings represent a complex interaction among anthropogenic and environmental conditions that influence mortality, the probability of washing ashore and the probability of being reported (Nero et al. 2013, Santos et al. 2018). Nonetheless, we presume that the more turtles present in an area, the more likely it is that one will wash ashore and be reported; thus, annual differences in the number of strandings are likely to be related to turtle abundance across that region (Hart et al. 2006). Owing to the inherent limitations of interpreting strandings data (Baskale et al. 2018, Lalire and Gaspar 2018), we aggregated strandings over large spatial extents (> 500 km of coastline) and temporal periods (annually), to damp higher-frequency signals associated with pulses in sea turtle mortality (Santos et al. 2018, Foley et al. 2019).

We aggregated strandings data into four regions: 1) Campeche, MX and Yucatan, MX, 2) Texas, USA, 3) Louisiana USA, Mississippi, USA and Alabama, USA and 4) western Florida, USA (Fig. 1, Supplementary material Appendix 1 Table A3). We included any recorded Kemp's ridley, green and loggerhead turtles that measured ≤ 38 cm curved carapace length (CCL). This size reflects higher growth rates for Kemp's ridley compared to the other species and is consistent with the wide range of size/age estimates for turtles in the oceanic-stage or that have recently recruited to coastal waters (Reich et al. 2007, Goshe et al. 2010, Scott et al. 2012, Avens et al. 2015, 2017, Metz and Landry 2016). Annual stranding records were available for comparison to model predictions for all years (1996–2017, n = 22 yr) from the U.S. regions, owing to long-term coordination of the Sea Turtle Stranding and Salvage Network (Shaver and Teas 1999). Stranding records in Campeche–Yucatan, however, were only available for 1997–2004, 2006, 2008 and 2012–2017 (n = 16 yr). In Campeche–Yucatan, no loggerhead and only two Kemp's ridley strandings were recorded. Thus, no statistical analyses were performed for these two species in this region. The aggregate dataset comprised records for 2576 Kemp's ridley, 8242 green turtles and 539 loggerhead turtles. These strandings were compared to our model's predicted abundances that were summed across the 1° latitude × 1° longitude grid cells along the coastline for the four stranding regions (Fig. 1).

We used the Spearman rank-order correlation (nonparametric) test to determine whether years with high predicted juvenile sea turtle abundance were also years with high strandings of turtles ≤ 38 cm CCL (and vice versa). We performed these correlations at the level of species (e.g. the

summed predicted abundance of all modeled Kemp's ridley nesting aggregations) and individual nesting aggregations (e.g. the predicted abundance for Texas, Tamaulipas and Veracruz separately). This allowed us to explore the strength of connectivity between each nesting and each coastal recruitment area (Fig. 1).

Results

Dispersal simulations revealed similarities in the spatial distributions of Kemp's ridley, green and loggerhead turtles during their oceanic stage (Fig. 2–5). Some common features of predicted turtle distributions were a tendency for higher densities in the northern Gulf of Mexico compared to the southern, and a high-degree of temporal variability in turtle densities (with standard deviations routinely exceeding mean values). Areas of high density differed by age class of species. Relatively high densities of Kemp's ridleys were predicted across western Gulf of Mexico (age 0.5 yr), the western and central northern Gulf of Mexico (ages 1.5–2.5 yr), extending eastward to west Florida (age 2.5 yr), with some portion concentrating offshore of northeast Florida and North Carolina (age 1.5 yr) (Fig. 5A–C). High abundances of green turtles were predicted in the southeastern Caribbean Sea (ages 0.5–3.5 yr), the U.S. Atlantic coast (ages 0.5–1.5 yr), the northern Gulf of Mexico (ages 1.5–3.5 yr) and within the Sargasso Sea (ages 2.5–3.5 yr) (Fig. 5D–G). Loggerheads were predicted to occur in high numbers in the eastern Gulf of Mexico (ages 0.5–1.5 yr), along the eastern U.S. coast and northwestern Atlantic (0.5 yr) and within the Sargasso Sea (ages 1.5–3.5 yr) (Fig. 5H–K).

Other distinct spatial patterns among species were also evident. For instance, increasing trends of turtle density were observed during 1996–2017 for all three species in the northern Gulf of Mexico, but the highest increases for Kemp's ridley density occurred along the Texas shelf and offshore of eastern Louisiana, Mississippi and Alabama (Fig. 2C). For green turtles, the highest increases in density were along the Texas shelf and Florida panhandle (Fig. 3C). Loggerhead density increased most along the nearshore waters of eastern Louisiana, Mississippi and Alabama (Fig. 4C). In the western Atlantic, increasing densities of Kemp's ridley were predicted along northeast Florida and along the North Carolina coast (Fig. 2C), green turtle densities increased along the North Carolina coast and further offshore following the Gulf Stream (Fig. 3C), while loggerhead densities showed increases in northeast Florida and off the Georgia coast (Fig. 4C).

Relationships between predicted oceanic-stage turtle abundance across the coastal regions of the Gulf of Mexico and strandings of young turtles (≤ 38 cm CCL) also varied considerably among species (Fig. 6, Supplementary material Appendix 1 Table A4). Total predicted abundance of Kemp's ridleys was correlated with strandings along western Florida (Spearman $r = 0.52$, $p = 0.01$), but not other regions. At the scale of individual nesting regions, predicted abundance of Kemp's ridley from Tamaulipas and Veracruz populations

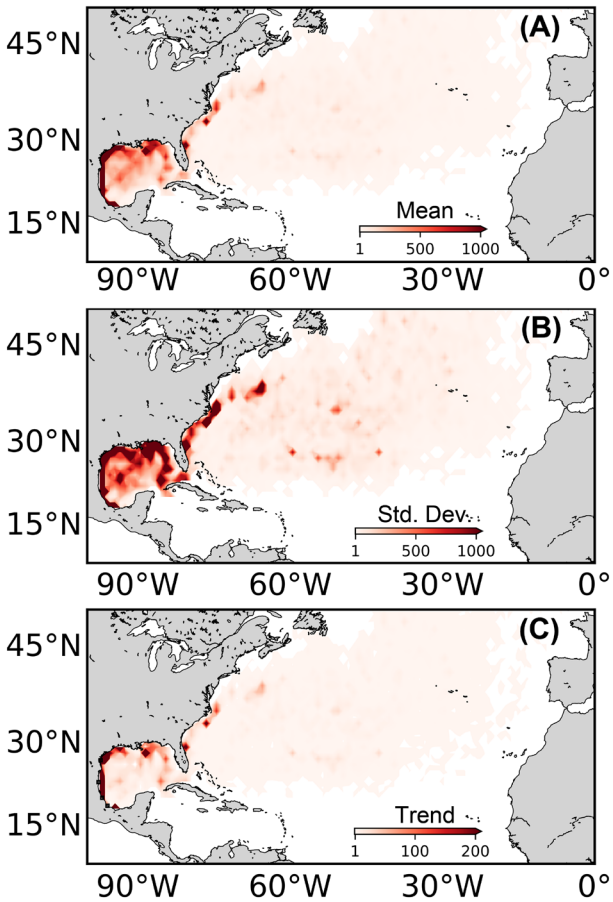

Figure 2. Maps of predicted oceanic-stage Kemp's ridley density derived from dispersal simulations weighted by estimates of hatchling production and survival from 1996 through 2017 in 1° latitude × 1° longitude bins. (A) Depicts the mean annual number of turtles in each bin. (B) Shows the absolute value of the annual standard deviation of mean density. (C) Indicates the increase in the number of turtles each year (positive trend) by location.

each correlated with western Florida strandings (Spearman $r > 0.45$, $p = 0.03$, for both comparisons), but not the other regions. Predicted abundance of Kemp's ridley from Texas only correlated with strandings in Texas (Spearman $r = 0.58$, $p < 0.01$) (Fig. 6A). Predicted green turtle abundance was correlated with strandings along all four regions in the Gulf of Mexico (Spearman $r > 0.42$, $p < 0.05$, for each comparison). Along the Campeche-Yucatan coast, green turtle strandings were correlated with predicted abundances arriving from all nesting regions (Spearman $r > 0.6$, $p < 0.01$) except Costa Rica (Spearman $r = 0.24$, $p = 0.36$). Along the Texas coast, green turtle strandings were correlated with predicted abundances from Campeche, Yucatan, Quintana Roo and Costa Rica nesting regions (Spearman $r > 0.54$, $p < 0.01$, for each comparison). Across the Louisiana–Alabama coast, predicted green turtle abundance from southwest Florida, Campeche, Yucatan and Costa Rica correlated with strandings (Spearman $r > 0.50$, $p < 0.01$, for each comparison) (Fig. 6B). Along western Florida, there were no correlations between green

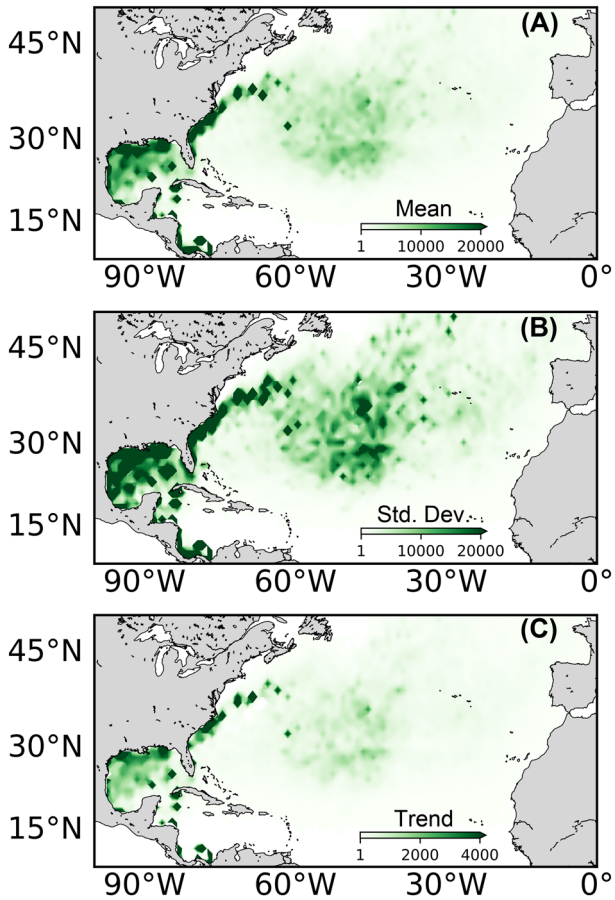

Figure 3. Maps of predicted oceanic-stage green turtle density derived from dispersal simulations weighted by estimates of hatchling production and survival from 1996 through 2017 in 1° latitude × 1° longitude bins. (A) Depicts the mean annual number of turtles in each bin. (B) Shows the absolute value of the annual standard deviation of mean density. (C) Indicates the increase in the number of turtles each year (positive trend) by location.

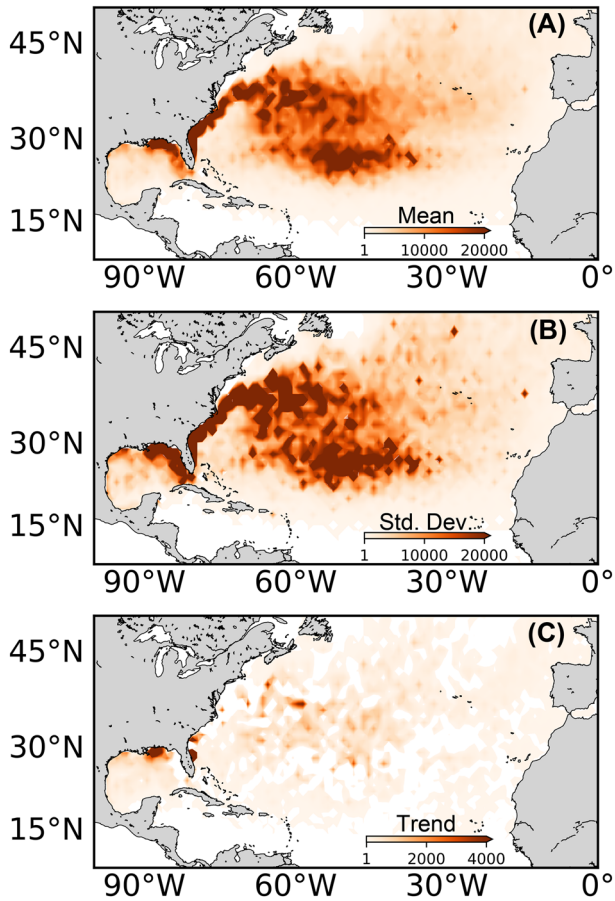

Figure 4. Maps of predicted oceanic-stage loggerhead turtle density derived from dispersal simulations weighted by estimates of hatchling production and survival from 1996 through 2017 in 1° latitude × 1° longitude bins. (A) Depicts the mean annual number of turtles in each bin. (B) Shows the absolute value of the annual standard deviation of mean density. (C) Indicates the increase in the number of turtles each year (positive trend) by location.

turtle strandings and individual nesting regions (Spearman $r < 0.39$, $p > 0.07$, for each comparison). For loggerheads, neither the aggregate predictions of abundance nor the predictions for individual nesting sites correlated with strandings (Spearman $r < 0.39$, $p > 0.07$, for each comparison) (Fig. 6C).

Discussion

Our results present a null hypothesis for oceanic-stage sea turtle densities over the past two decades that can provide context for in-water data obtained on turtle distributions and abundance. This model is based only on surface currents, mortality and hatchling production, which allows examination of how variability in sea turtle distributions results from ocean circulation processes. Given the limited information on this life-stage, but its apparent importance in determining the adult foraging areas, migration patterns, nesting grounds and overall abundance of sea turtle populations (Putman et al. 2010b, Scott et al. 2014, Putman 2018a, Caillouet 2019), our mechanistic movement model provides valuable insight into the spatial ecology of sea turtles across much of the North Atlantic (Fig. 2–5). We found that ocean currents across this region likely act to concentrate large numbers of young turtles within particular regions (Fig. 2A, 3A, 4A). However, temporal variation in abundance within these regions may be high, both as a result of dynamic ocean conditions and variable hatchling production (Fig. 2B, 3B, 4B). In addition, many nesting sites have seen an increase in nest abundance as a result of long-term conservation efforts (Mazaris et al. 2017). Our model indicates increasing nest abundances for Kemp's ridley and green turtles propagate to distant regions (Fig. 6), with the highest rates of increase often occurring in coastal regions in the northern Gulf of Mexico and eastern U.S. coast (Fig. 2C, 3C, 4C). Implementing successful management, conservation, and restoration strategies for sea turtles will thus require international coordination (Hamann et al. 2010) and this model

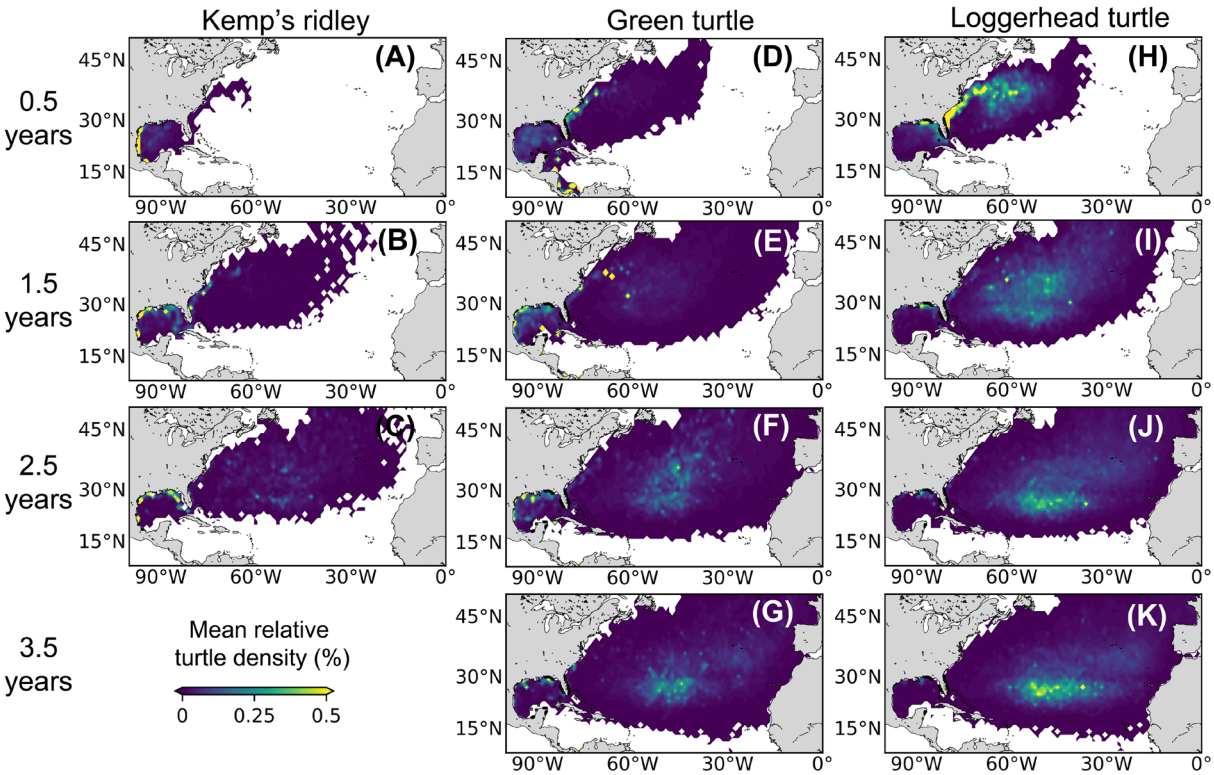

Figure 5. Maps showing the predicted mean percentage of oceanic-stage (A–C) Kemp's ridley, (D–G) green and (H–K) loggerhead turtles in 1° latitude × 1° longitude bins, derived from dispersal simulations weighted by estimates of hatchling production and survival from 1996 through 2017. The distribution of turtles are shown separately by age: (A, D, H) 0.5 yr old turtles, (B, E, I) 1.5 yr old turtles, (C, F, J) 2.5 yr old turtles and (G, K) 3.5 yr old turtles.

can help identify potential areas of common interests among countries (Putman et al. 2015).

Comparison of model predictions to observations

Agreement between model predictions and Kemp's ridley strandings in west Florida highlight west to east connectivity in the Gulf of Mexico (Fig. 6A) and suggest temporal variability of recruitment into this region may depend upon ocean circulation processes that influence the transport of young turtles departing Tamaulipas and Veracruz (Sansón et al. 2017). The lack of correlation at the species-level for the more western regions in the Gulf may reflect an aspect of the movement ecology of young Kemp's ridley that is missing from our model. For instance, if post-hatchling Kemp's ridleys steadily swim eastward as they depart their nesting beaches in Tamaulipas and Veracruz (Putman and Mansfield 2015), many might exit the northward currents along the shelf that would tend to transport large numbers of turtles into Texas and Louisiana waters. In contrast, a strong correlation between the modeled Texas Kemp's ridley population and Texas strandings was detected (Supplementary material Appendix 1 Table A4). An intriguing possible explanation is that this small, but increasing nesting aggregation (Shaver and Caillouet 2015) contributes disproportionately to the young turtles that occupy and recruit to these waters because surface currents encountered by post-hatchlings from Texas tend to be more retentive than dispersive (Putman et al. 2010a, Caillouet et al. 2015, Putman 2018a).

The predictions from the movement model corresponded particularly well to strandings of small green turtles (Fig. 6B, Supplementary material Appendix 1 Table A4), suggesting that temporal variability in green sea turtle strandings across the Gulf of Mexico are likely associated with oceanic-to-coastal recruitment dynamics, driven by ocean circulation. Predicted connectivity from this movement model (Fig. 6B) also appears consistent with existing data on the genetic structure of green turtles. For instance, the mitogenomics of stranded green turtles in Texas point toward origins from Mexico and Costa Rica, rather than Florida (Shamblin et al. 2017) and our model's predictions of juvenile inputs to Texas from nesting beaches across Mexico and Costa Rica (but not Florida) are closely related to green turtle strandings (Supplementary material Appendix 1 Table A4). For the eastern Gulf of Mexico, genetic analyses of green turtles indicate inputs from populations in Mexico, Costa Rica and Florida, though proportions may vary over time or sub-regionally (Foley et al. 2007, Naro-Maciel et al. 2017, Shamblin et al. 2018). In our simulations, no individual green turtle population's predicted juvenile inputs to Florida were correlated with strandings, but when population inputs were considered in aggregate there was a significant correlation (Supplementary

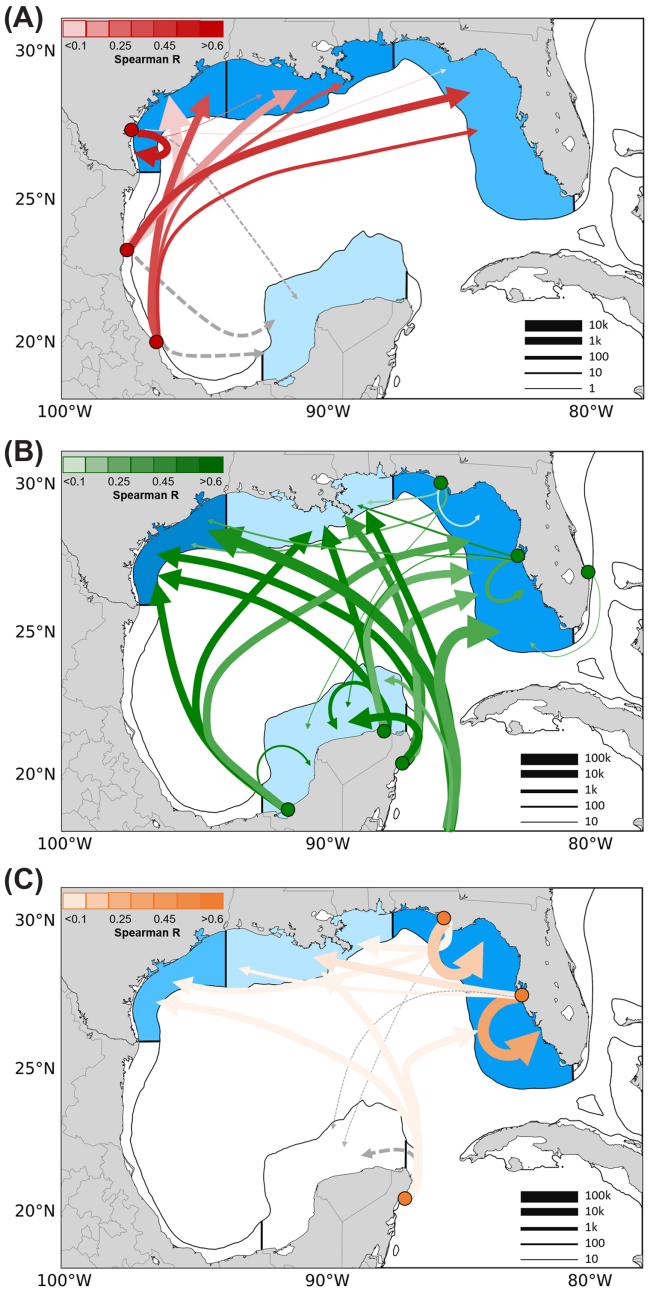

Figure 6. Schematic of the relationships between predicted inputs of oceanic-stage sea turtles into coastal regions and observed strandings. Darker shading of blue indicates regions with more stranding records (Supplementary material Appendix 1 Table A3). Arrow width indicates the mean abundance of predicted turtles arriving from a nesting area, coloration indicates the correlation between predicted abundance and strandings; dashed grey lines indicate that a lack of stranding data precluded correlations (Supplementary material Appendix 1 Table A4). (A) Kemp's ridley; (B) green turtles, with arrows from the Caribbean Sea representing Costa Rica; and (C) loggerhead turtles.

material Appendix 1 Table A4). Thus, green turtle recruitment along the West Florida Shelf may fluctuate between large numbers of inputs from distant (Mexico, Costa Rica) and local (Florida) sources depending upon the state of the Loop Current (Candela et al. 2002, Miron et al. 2017) and hatchling production across these widely separated nesting sites.

No strong relationships were detected between loggerhead strandings and our model's predictions of abundance (Fig. 6C, Supplementary material Appendix 1 Table A4). This difference compared to Kemp's ridley and green turtle strandings likely reflects a difference in species life-histories. Loggerheads do not typically recruit to nearshore waters at the maximum ages modeled in this study (3.5 yr), whereas both Kemp's ridley and green turtles do (Reich et al. 2007, Scott et al. 2012, Avens et al. 2015, 2017). Indeed, despite the large abundance of hatchlings produced (Supplementary material Appendix 1 Table A1), over the 22-yr period only 539 stranding records were available for loggerheads ≤ 38 cm CCL (on average ~6 records per year, per region) compared to 2576 Kemp's ridley (~29 records per year, per region) and 8242 green turtles (~94 records per year, per region). The few stranding records for loggerhead turtles suggest that their occurrence in coastal waters at this size-class is unusual and may be driven by atypical events. For instance, this result mirrors findings from northern France, in which the strandings of loggerhead turtles were not explained by ocean current transport, but by the occasional influence of tropical storms (Monzón-Argüello et al. 2012). Regardless of the processes that ultimately determine the strandings of loggerheads, the small sample size for loggerheads makes detecting a relationship difficult. Thus, the disagreement between loggerhead strandings and predicted abundances do not necessarily indicate that the modeled distributions of loggerheads are fundamentally flawed. Compared to Kemp's ridley and green turtles, the movements of loggerheads may be more closely tied to migrating to the North Atlantic Subtropical Gyre (Monzón-Argüello et al. 2009, Putman et al. 2012, Martins et al. 2018, Chambault et al. 2019) than remaining within the Gulf of Mexico. Our model results are consistent with this view, in that high abundances of loggerheads are predicted to enter the Sargasso Sea (Fig. 4A), similar to what has been observed in satellite-tracked loggerheads of comparable age (Mansfield et al. 2014). Likewise, the model predicts relatively high variability in loggerhead abundance around the Azores (Fig. 4B), but no trend through time (Fig. 4C), as do at-sea surveys (Vandeperre et al. 2019).

Application and future directions

Nest counts (and thus likely hatchling production) are increasing for most sea turtle populations in this region (Mazaris et al. 2017) and our results suggest that increases of in-water abundance will be much greater in some places than others (Fig. 2–5). Though our model predicts large numbers of oceanic stage sea turtles across the North Atlantic, even in regions where predictions of abundance are relatively high (e.g. upwards of 20 000 turtles per 1° of latitude by 1° of longitude) this equates to densities of no more than 1–2 turtles km^{-2}. Such low densities limit the

practicality of large-scale oceanic surveys and thus highlight how these simulations could extend the utility of observations obtained over more limited areas (Witherington et al. 2012, Vandeperre et al. 2019). For instance, the simulations presented here could contribute to the designation (Kemp's ridley and green turtles) or revision (loggerhead turtles) of juvenile 'critical habitat' under the U.S. Endangered Species Act (50 CFR § 226.223 2014). Likewise, this work could aid in the management of the numerous anthropogenic activities in the northwestern Atlantic Ocean and potentially interact with sea turtles. Relevant activities include oil spills (Vander Zanden et al. 2016, Reich et al. 2017, Wallace et al. 2017); the removal of oil and gas platforms from the northern Gulf of Mexico (Rezek et al. 2018); the development of marine energies (e.g. wind, tidal current and wave) along the eastern U.S. coast (Bonar et al. 2015, Stone et al. 2017); dredging, sediment diversion and sand mining along the Louisiana coast (Stone et al. 2004, Sha et al. 2018); and seagrass restoration (Thorhaug et al. 2017) among others. These models may be particularly useful for giving an indication whether fisheries bycatch of sea turtles in certain areas is increasing or decreasing due to management actions (e.g. reducing effort, gear modifications) or because of a change in turtle distributions and abundance (Lewison et al. 2014).

Our predictions of turtle distributions could be also applied as inputs to a suite of other modeling approaches that would benefit from increased detail on the proportion of hatchling cohorts that experience different environmental conditions or anthropogenic disturbances. For instance, combining our movement model with a mechanistic model of heat and momentum balance (Dudley et al. 2014) and dynamic energy budget model (Marn et al. 2017, Stubbs et al. 2019) could improve estimates of how changes in the distributions of oceanic-stage turtles influence growth, survival and reproductive output in individual turtles. Aggregating such information by year classes could then feed into population dynamics (Warden et al. 2015), stock assessment (Gallaway et al. 2016) or ecosystem (Gruss et al. 2018) models to determine the potential influences on population abundance, age-structure and resiliency.

The movement modeling approach to predict sea turtle distributions, as presented here, is relevant to numerous marine taxa in which locations of reproductive grounds are known and time-series of juvenile abundance are available. With only minor modifications to our methods similar investigations could be conducted for species as diverse as tuna (Domingues et al. 2016), salmon (Burke et al. 2013, Fergusson et al. 2013), penguins (Tivelpiece et al. 2011, Abadi et al. 2017) and seals (Forcada et al. 2005, Reijnders et al. 2010). As this approach to predicting animal distributions is more widely applied, further development of these movement models would benefit from continued basic research in marine animal behavior and physical oceanography. Incorporating species-specific (Putman and Mansfield 2015) and population-specific (Christiansen et al. 2016, Mansfield et al. 2017) swimming behavior, with explicit consideration for the sensory-basis of movement decisions in animals (Putman et al. 2012), is likely to improve the model's skill (Putman 2018a). Likewise, efforts to refine the representation of physical ocean circulation processes will yield better insight into the mechanisms shaping organismal distributions (Putman 2018b).

Data availability statement

Model predictions of sea turtle distribution/abundance is publicly available at VirTu, the juvenile sea turtle density estimator tool <https://virtu.mesophotic.ccs.miami.edu>. The 1/12 deg global HYCOM + NCODA Ocean Reanalysis used in this paper was funded by the U.S. Navy and the Modeling and Simulation Coordination Office and is publicly available at <http://hycom.org>.

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Supplementary material (available online as Appendix ecog-04929 at <www.ecography.org/appendix/ecog-04929>). Appendix 1.