



Oceanic drivers of juvenile sea turtle strandings in the UK

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ABSTRACT: Juvenile sea turtles can disperse thousands of kilometers from nesting beaches to oceanic development habitats, aided by ocean currents. In the North Atlantic, turtles dispersing from American beaches risk being advected out of warm nursery grounds in the North Atlantic Gyre into lethally cold northern European waters (e.g. around the UK). We used an ocean model simulation to compare simulated numbers of turtles that were advected to cold waters around the UK with observed numbers of turtles reported in the same area over ~5 decades. Rates of virtual turtles predicted to encounter lethal (10°C) or detrimental (15°C) temperatures (mean 19% ± 2.7 SD) and reach the UK were consistently low (median 0.83%, lower quartile 0.67%, upper quartile 1.02%), whereas there was high inter-annual variability in the numbers of dead or critically ill turtles reported in the UK. Generalized additive models suggest inter-annual variability in the North Atlantic Oscillation (NAO) index to be a good indicator of annual numbers of turtle strandings reported in the UK. We demonstrate that NAO variability drives variability in the dispersion scenarios of juvenile turtles from key nesting regions into the North Atlantic. Coastal effects, such as the number of storms and mean sea surface temperatures in the UK, were significant but weak predictors, with a weak effect on turtle strandings. Further understanding how changing environmental conditions such as NAO variability and storms affect the fate of juvenile turtles is vital for understanding the distribution and population dynamics of sea turtles.

KEY WORDS: Sea turtle · Stranding · North Atlantic Oscillation · NAO · Dispersal · Ocean model · Storms effects

1. INTRODUCTION

Small organisms such as insects, marine larval life stages and juvenile sea turtles utilize air and water flows to disperse away from natal sites to development and/or settlement sites (Kinlan & Gaines 2003, Siegel et al. 2003, North et al. 2008, Chapman et al. 2010, Monzón-Argüello et al. 2010). They can disperse over tens to tens of thousands of kilometers and

have evolved a variety of behaviors to help ensure that they remain in favorable habitats. Insects and planktonic larvae can vary their vertical position to remain in favorable flows (North et al. 2008, Chapman et al. 2010) whilst larger animals like juvenile sea turtles embark on periods of directed horizontal swimming in response to a range of environmental cues (Fisher et al. 2005, Lohmann et al. 2008, Fuxjager et al. 2011). Due to their small size and wide-

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spread dispersal in oceanic habitats, little is known about the ecology of juvenile sea turtles, but understanding how oceanic variability affects their fate is vital because juvenile dispersal shapes the dynamics, distributions and behaviors of later life stages (Scott et al. 2014b, Ascani et al. 2016).

When newly hatched sea turtles first enter the ocean, an initial 'swimming frenzy' helps them to escape shallow coastal water (Wyneken & Salmon 1992) and reach favorable offshore current flows (Putman et al. 2012a). This marks the beginning of a dispersal phase known as the 'lost years' (after Carr 1952), during which turtle hatchlings disperse into the pelagic realm (e.g. Scott et al. 2014a). However, reports of juvenile turtles caught by fishers as bycatch and dispersal simulation studies provide insights into their whereabouts and have confirmed that surface ocean current systems drive their dispersion (e.g. Blumenthal et al. 2009, Boyle et al. 2009, Monzón-Argüello et al. 2009, 2010). In the North Atlantic, juvenile loggerhead sea turtles *Caretta caretta* traverse the entire ocean basin during their development phase, as shown by matching genetic signatures of juvenile turtles found in development habitats around the Azores archipelago to American nesting populations (Bolten et al. 1998, Monzón-Argüello et al. 2009, LaCasella et al. 2013). The east coast of America hosts one of the world's largest aggregations of nesting loggerhead sea turtles, spanning from Florida to North Carolina, with the majority of nests (90%) concentrated in southeast Florida (Murphy & Hopkins 1984, Casale & Tucker 2015). Sea turtles originating from this population, as well as Kemp's ridley *Lepidochelys kempii* and green turtles *Chelonia mydas*, use the Gulf Stream and North Atlantic subtropical gyre to disperse to warm oceanic development habitats in the North Atlantic basin (e.g. around the Azores archipelago; Wyneken et al. 2008, Monzón-Argüello et al. 2010, Putman et al. 2010, 2012a, 2020, Scott et al. 2012a).

However, due to their small size, juvenile turtles risk being advected to unfavorable habitats. Therefore, hatchlings have evolved directional swimming behaviors to help them stay in warm waters (Putman et al. 2012b, Scott et al. 2012a). Sea turtles are ectothermic, their body temperature is regulated by water temperature, and laboratory experiments indicate that hatchling loggerhead turtles become inhibited in their ability to swim (they become cold-stunned) at temperatures below 15°C and that temperatures of 10°C and below are fatal (Schwartz 1976, Davenport et al. 1997). If their ability to swim is inhibited due to cold-stunning (Davenport et al. 1997), they risk being advected with currents like the North Atlantic Cur-

rent and/or storms towards northern Europe. For example, there are records dating back to ca. 1758 of cold-stunned juvenile sea turtles (predominantly loggerhead sea turtles) in the UK.

The oceanographic systems that hatchlings rely on for transport are subject to spatial and temporal variability (e.g. Richardson 1985, Meinen et al. 2010, Scott et al. 2017). For example, in the North Atlantic, the strength of westerly winds modulates north and westward transport of key surface water masses on inter-annual and decadal timescales such as the Gulf Stream and North Atlantic Current. The wind-driven gyre circulation in the North Atlantic responds to changes in the atmospheric forcing, which are captured in the North Atlantic Oscillation index (NAO). Climatic indexes can be a useful indicator of climate modes and factors that influence ecological processes (Ottersen et al. 2001, Visbeck et al. 2003, Ascani et al. 2016). Oceanic variability, particularly in ocean currents, has been proposed as a potential explanation for reports of cold-stunned turtles stranding in the UK, as stranding reports show high inter-annual variability (Witt et al. 2006), and the genetic signature of stranded turtles in Europe has been traced back to nesting populations in America (Monzón-Argüello et al. 2012).

Ocean models have become a well-established tool to study the cryptic pathways and the fate of small marine organisms, like sea turtle hatchlings, that are too small to track directly (Putman et al. 2012b, Baltazar-Soares et al. 2014, Scott et al. 2014a). Here we use an oceanographic model to simulate the dispersal of hatchlings to investigate if inter-annual variability of observed stranding numbers in the UK could be explained by variations in simulated and observed oceanographic conditions. We assess how potential environmental drivers affect observed stranding variability and how estimated temperature-induced mortality rates of drifting juvenile turtles relate to stranding events, drift pathways and expected mortality. Loggerhead turtles dominated in the stranding records of juvenile turtles reaching the UK; hence, we used loggerhead turtle nesting regions and seasons as the spatial and temporal focus of our drift simulations.

2. MATERIALS AND METHODS

2.1. Reports of juvenile sea turtles stranding in the UK

We obtained reports of sea turtles stranding in the British Isles from the TURTLE database operated by Marine Environmental Monitoring (available through

Rod Penrose) where turtle strandings are compiled as part of the UK Cetacean Strandings Investigation Programme (CSIP). TURTLE, established in 2001, logs validated reports of sea turtles stranding on UK beaches or occurring in UK waters from members of the public, governmental agencies, and marine environmental organizations. The database also includes historic reports of sea turtles in the UK since ca. 1758 gleaned from published literature (Brongersma 1972, Penhallurick 1990), unpublished data and governmental reports. Whilst precise stranding locations were not known, we used observational reports (dead, alive, stranded and at sea sightings) of juvenile turtles encountered around the UK between 1960 to 2014 match with the period for which we had high resolution oceanographic model results. Our analysis included 182 reports for all 3 species of hard-shelled turtle which were subjected to cold-stunning (between 1960 and 2014: 92 loggerhead turtles *Caretta caretta*, 20 Kemp's ridleys *Lepidochelys kempii*, 5 green turtles *Chelonia mydas*, and 65 turtles of unknown species, the majority of which [40] were confirmed hard-shelled turtles). Given the high proportion of loggerhead turtles among the records identified to species level, we assumed that this species was also dominant among the unidentified records, and hence we also included the unidentified turtle records in our analyses. All 3 species use the North Atlantic Gyre for dispersion and spend the first years in pelagic habitats, although the loggerhead turtle is the most common species in this system (Putman et al. 2020).

We only included juvenile turtles (size classification in accordance with Bjorndal et al. 2000, Bolten 2003), i.e. if they measured <60 cm in carapace length (using both straight and curved carapace length measures). When carapace length was not available, we included records of total length <80 cm (records with size measured: $n = 157$). We also included records that were classified as 'small' ($n = 19$) or 'juvenile' ($n = 6$) in the notes section of records that did not have exact measurements. The number of stranded juvenile turtles was determined by summing up the number of records meeting the above outlined criteria for each year. Based on the size distribution of juvenile turtles with reported size information, the median size was 32 cm (across measurement types, including straight carapace length, curved carapace length, total estimated size; Fig. 1). Previous studies have estimated the mean age of the stranded turtles in northern Europe between 1.8 and 3.75 yr (Witt et al. 2006, Scott et al. 2012b). However, age estimates of cold-stunned individuals are caveated by the fact that growth rates are influenced by temperature and inhibited in cold temperatures (Scott et al. 2012b).

2.2. Ocean model set up

We used an ocean model (VIKING20) to obtain drift trajectories for virtual particles (virtual turtles). Our model comprised a 2-way nesting scheme (Debreu et al. 2008) using a high resolution ($1/20^\circ$) North Atlantic grid spanning 32° and 85° N (VIKING20; Böning et al. 2016) nested within a coarser ($1/4^\circ$) global ocean/sea-ice model (ORCA025; Fichefet & Maqueda 1997, Barnier et al. 2006). The atmospheric forcing that drives the model used bulk formulations and data products (1948–2009) as suggested by the Co-ordinated Ocean-ice Reference Experiments (CORE2, 6-hourly wind speed, humidity and atmospheric temperature; Large & Yeager 2008, Griffies et al. 2009). The global model was initialized using a temperature and salinity climatology (Levitus et al. 1998). After a 30 yr spin-up period, during which the model equilibrates, a hindcast experiment for the nested VIKING20 model was conducted (1948–2007). We excluded the first 12 yr of hindcast data to exclude secondary spin up effects which can result

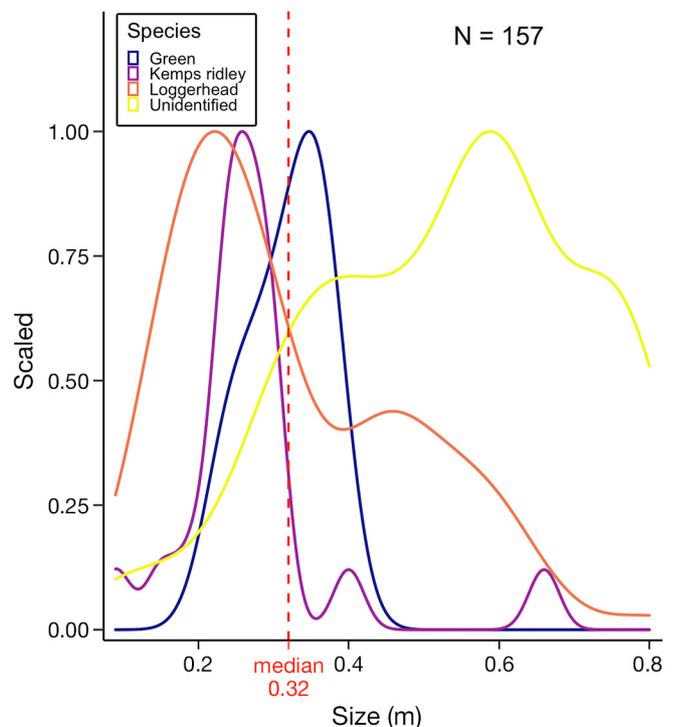


Fig. 1. Size distribution of 157 records of juvenile sea turtles stranded or sighted in the UK included in this study, for which size measurements were available. Presented as smoothed kernel density distribution of size (m) for each species. Red dashed line: median size of 0.32 m. We excluded 25 records for which size measurements were not available (but turtles were included based on information in the notes section of each record in the TURTLE database). Density lines are colored by species identification of each record

from the initialization of the nested model. We thus obtained current fields and temperatures of the surface layer, defined as the upper 6 m grid box in the model, for 1960–2007, which were stored as 5 d averages. The ocean model VIKING20 has been set up and validated to accurately represent oceanic current and water mass variability of the North Atlantic of the past decades (Behrens 2013, Breckenfelder et al. 2017). The model has been extensively used to explore the Atlantic Ocean circulation variability (Böning et al. 2016, Breckenfelder et al. 2017) and as an input for dispersal studies about juvenile eels (Baltazar-Soares et al. 2014) and deep-sea mussels (Breusing et al. 2016), both following the same technique (see Section 2.3).

2.3. Hatchling dispersal simulations

To simulate juvenile turtle dispersion in the ocean model, we released virtual turtles into the ocean model current fields, using the particle tracking software ARIANE (<http://stockage.univ-brest.fr/~grima/Ariane/>; Blanke et al. 1999). We released 1659 virtual turtles every 5 d during the 4 mo-long hatching season of loggerhead turtles (July to October) from 1960 to 2009, resulting in 41 475 virtual turtle dispersion trajectories per year, released in every second model grid box in both the *x* and *y* direction. The release grid spanned a region off the east coast of the USA (73–80° W and 32–34° N; Fig. S1 in Supplement 1 at www.int-res.com/articles/suppl/n048p015_supp.pdf), a key region through which hatchlings from the major loggerhead sea turtle nesting beaches in our study region would drift following an initial offshore swimming frenzy. Hatchlings of other sea turtle species that nest in the northwest Atlantic and use the North Atlantic Gyre for dispersion (i.e. green and Kemp's ridley turtles from southeast USA and the Gulf of Mexico (Putman & Naro-Maciel 2013, Putman et al. 2020) would also pass through this region. Near shore coastal waters are not well represented in the model, and it is therefore important to release virtual turtles in or near major ocean currents.

Virtual turtles were passively advected in the surface flow fields, and their positions and associated water temperature were reported every 5 d for the first 2 yr of drift, the time during which juvenile turtles would be most vulnerable to displacement (e.g. Putman et al. 2020). Turtle hatchlings are positively buoyant (Milsom 1975) and found primarily in surface waters, so the virtual turtles were restricted to the surface layer (upper ~6 m). The number of virtual

turtles (i.e. 'simulated arrivals') in the UK was determined by counting virtual turtles reaching within 2 km of the coast, summed over each year.

2.4. Mortality estimates

We used the temperatures that virtual turtles experienced along their dispersion paths to estimate temperature-induced mortality rates. In accordance with Putman et al. (2012a), we assumed that during their first year of drift, when they are most vulnerable, virtual turtles experiencing temperatures of 10°C or lower die and that turtles encountering temperatures of 15°C or lower for 10 d or more have a 50% chance of survival. 'Mortality' is the number of virtual turtles that fit these criteria summed up per year.

2.5. Quantification of environmental drivers

To assess the possible influence of physical drivers on the fate of juvenile turtles (observed stranding records and simulated virtual turtles that reached UK waters), we quantified inter-annual variability of a range of environmental conditions using generalized additive models (GAMs, see Section 2.6 for model and GAM details). These variables were (1) the strength of the northward flow of the Gulf Stream (GS) and North Atlantic Current (NAC) (blue boxes in Fig. 2), (2) storms over the North Atlantic (storm index), (3) the NAO, (4) regional storms around the UK (storm count) and (5) mean sea surface temperature (SST) around the UK. Sources and details are presented in Table 1 and Text S1 in Supplement 1, and all covariates are plotted in Fig. 3. In the GAMs, 'Storm_count' refers to the storm count per year around the UK. 'Storm_index' is the yearly number of time steps >2 SD above mean wind speed over the North Atlantic. To increase overlap with the observational period, we here used a more recent product (JRA55-do) than the atmospheric data which forces the model (COREv2). 'Mean_SST' is the yearly mean sea surface temperature calculated from 14 stations around the UK (°C), 'NAO_index' is the North Atlantic Oscillation index which is the difference of normalized sea level pressure (SLP) between Stykkisholmur/Reykjavik, Iceland, and Lisbon, Portugal. 'NAC transport' and 'GS transport' are the yearly maximum northward current transport of the North Atlantic Current and Gulf Stream, respectively, in Sverdrup. We checked for excessive autocorrelation between these predictor variables (Table S2 in Sup-

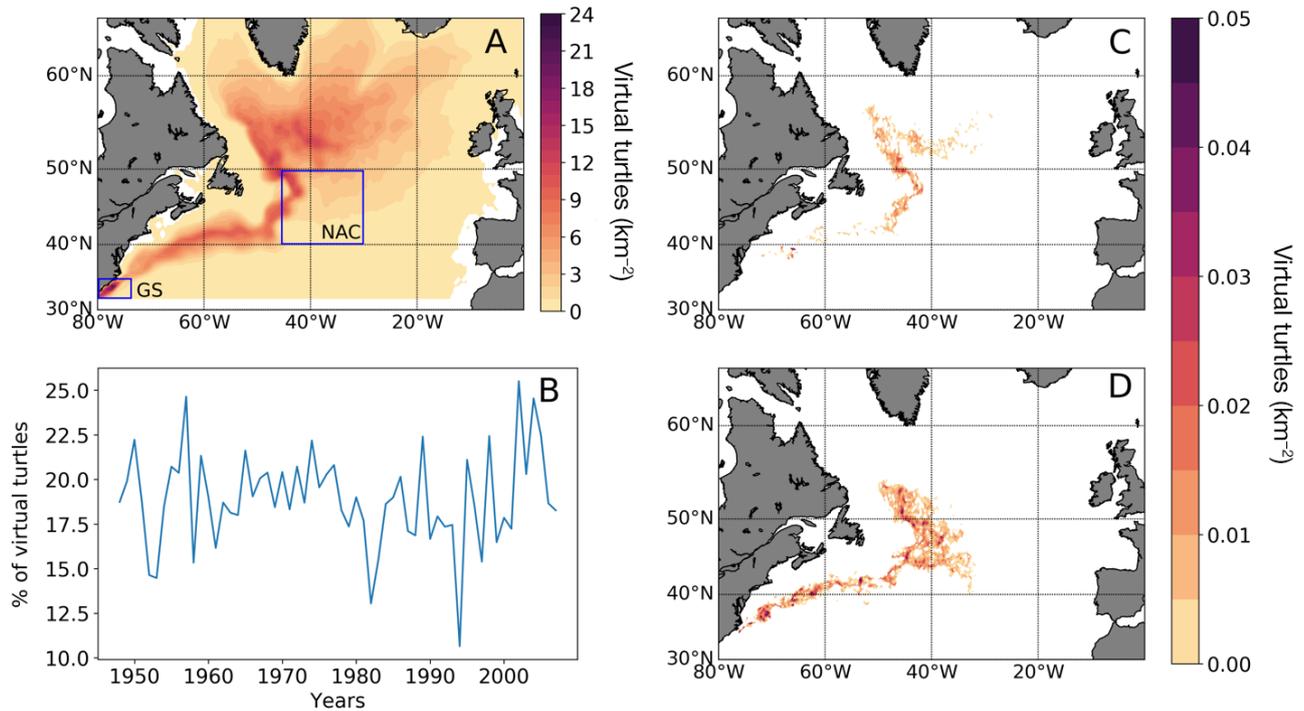


Fig. 2. Dispersal pathways of turtles' estimated mortality and distribution of mortality events. (A) Mean dispersal (virtual turtles km^{-2}) pathways of 'cold' virtual turtles, those encountering 10°C or less during their first year of drift, integrated over the 2 yr drift period. Blue boxes indicate where ocean current strength was obtained. (B) Model estimated mortality rates of virtual turtles in the North Atlantic Current (NAC) system (within first year of drift). It varies around a mean of $19\% \pm 2.7$ SD between 10.8 and 25.6%. Mortality was calculated under the assumption that 100% mortality occurs at ≥ 1 d of 10°C exposure, plus 50% mortality at ≥ 10 d of 15°C exposure, based on experimental data by Davenport et al. (1997). (C,D) Density distribution of locations where virtual turtles first encountered (C) 10°C and (D) 15°C

Table 1. Possible environmental drivers on the fate of juvenile loggerhead turtles assessed as predictor variables in generalized additive model analysis (GAMs). Units, data type and sources are presented; more details on the processing of these data can be found in Supplement 1 (Text S1). SST: sea surface temperature; NAO: North Atlantic Oscillation; GS: Gulf Stream; NAC: North Atlantic Current; SLP: sea level pressure; Sv: Sverdrup

Variable (units)	Variable name	Data	Sources
Storm events (count yr^{-1})	Storm_count	Regional storms over UK, events over 47 knots	Lamb & Frydendahl (1991) Met Office, UK Multiple sources: https://github.com/EllenJCoomb/cetacean-strandings-project
Storm index	Storm_index	Storms over the North Atlantic	JRA55-do, yearly count of 6-hourly time steps with wind > 2 SD from mean (Tsujino et al. 2018)
SST ($^{\circ}\text{C}$)	Mean_sst	Yearly mean SST around the UK (14 locations, Fig. S2 in Supplement 1)	Met Office: HadISST
NAO (mb)	NAO_index	Hurrell station-based index of normalized difference between SLP Stykkisholmur/Reykjavik, Iceland and Lisbon, Portugal	https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based
GS current (Sv), NAC (Sv)	GS transport, NAC transport	Maximum yearly northward transport derived from the horizontal streamfunction of 3D velocity fields in a representative area (Fig. 2A blue boxes)	VIKING20 model

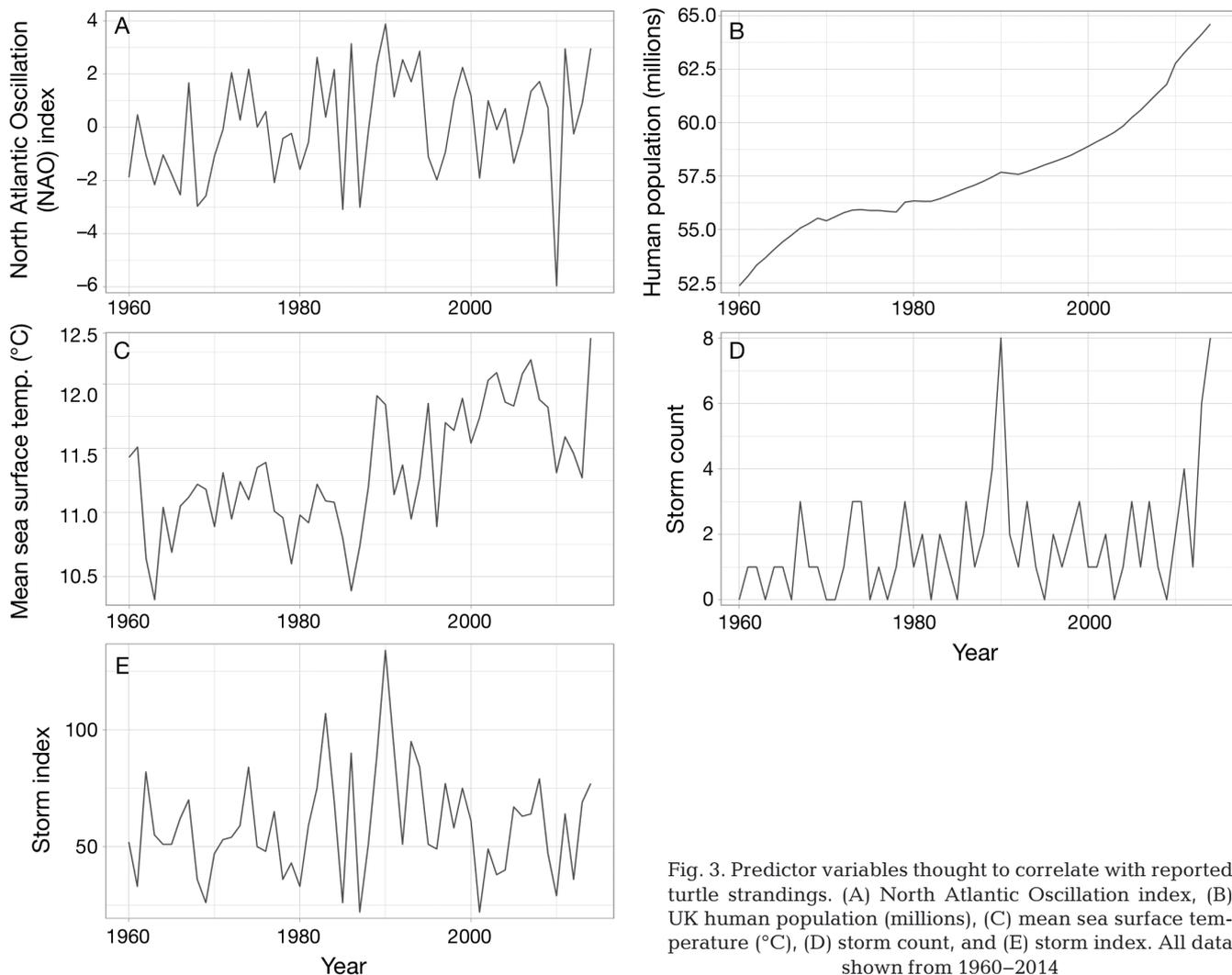


Fig. 3. Predictor variables thought to correlate with reported turtle strandings. (A) North Atlantic Oscillation index, (B) UK human population (millions), (C) mean sea surface temperature (°C), (D) storm count, and (E) storm index. All data shown from 1960–2014

plement 1) but found that values were not higher than expected for this type of data. To validate the selection of parameters obtained from the ocean model we also assessed the effect of physical drivers on the number of virtual turtles arriving to the UK within the ocean model (Table S1 in Supplement 1).

2.6. Generalized additive modelling

We used GAMs to assess the relationship between the numbers of observed turtles stranding in the UK (the response variable) and simulated numbers of virtual turtles arriving in the UK, temperature-induced mortality rate estimates, and physical drivers (outlined in Section 2.5). We ran 3 models to look for relationships between multiple explanatory variables and the response variable (turtle strandings). Details on the model checks and outputs for

Model 2 and Model 3 are included in Supplement 2 (at www.int-res.com/articles/suppl/n048p015_supp.pdf; summary of variables in Figs. S6 and S8, respectively, GAM checks in Figs. S7 & S9, respectively, and significance of smooth terms is presented in Table S1). The models were constrained to specific years due to the availability of data for each variable. We ran Model 1 with NAO, mean SST, storm count, and storm index as the predictor variables. The model was run from 1960–2014. We report the results using the Poisson distribution as this was the best fit for the data (compare Figs. S2 to S5 in Supplement 2). We ran Model 2 with GS transport and NAC transport as the predictor variables from 1960–2009. We report the results using the Tweedie distribution as this was the best fit for the data (Fig. S7 in Supplement 2). We ran Model 3 with mortality rate and simulated arrivals as the predictor variables from 1961–2007. We report the

results using the Tweedie distribution as this was the best fit for the data (Fig. S9 in Supplement 2).

We chose to run 3 separate models due to the increased uncertainty that arises when there are many covariates and few observations. Such complications can include highly uncertain estimated smooth functions. The more variables added to a model, the higher the number of coefficients—this becomes a problem when there are more coefficients than observations, especially for a small data set (i.e. 1961–2007).

GAMs allow for smoothed relationships between a response variable (here observed turtle strandings) and multiple explanatory variables (here simulations and environmental variables) (Wood 2011). We used GAMs because, unlike in a generalized linear model, the relationship between the predictors and response are not assumed to be linear (Wood 2011), making for a more flexible model especially when considering seasonal or cyclic variables. We used a link function to establish a relationship between the mean of the response variable and a ‘smoothed’ function of the predictor(s) (Guisan et al. 2002). To allow us to consider the effect of each term on the response individually, we modelled smooths using a thin plate spline basis with shrinkage (Marra & Wood 2011) so that during the initial stages of model fitting each term is removed in turn from the model (i.e. the effect size is shrunk to zero). The same was done for time (‘Year’) in the model; see below for details.

To account for changes in sampling effort we included yearly UK human population size as an offset in the model (Fig. 3B). Previous stranding studies showed the importance of considering observer effort and the use of human population growth as a proxy (Maldini et al. 2005, Witt et al. 2006, Pyenson 2011, Coombs et al. 2019). We thus used annual UK human population data as in Coombs et al. (2019), who analysed cetacean stranding reports around the UK and Irish coast. As human population size increases, animals arriving to UK coasts or in UK waters are most likely detected, observed, and reported more frequently (Coombs et al. 2019). It is also important to note that a reporting scheme for strandings was initiated in 2001 which would increase the probability of strandings to be reported officially and which has increased public visibility of the issue over the time of its existence. However, the TURTLE database includes records gleaned from historical sources. An initial review of the data showed an increase in stranding numbers towards the present day, while the variability observed in earlier years persisted (i.e. some recent years report no strandings). We therefore added a smooth of time (‘Year’) to our models. By

allowing a smooth of ‘Year’ we can remove the effect of year from the model and instead focus on the effects of the other predictors one at a time.

The total number of observed stranded individuals were modelled using GAMs with the general formulation:

$$s_t = \exp \left[\log(p_t) + \beta_0 + \sum_{j=1}^J f_k(z_{tj}) \right] \quad (1)$$

where s is the number of stranded individuals, t is year, p is an offset of human population size, β_0 is the intercept and f_k are smooths of the J explanatory variables, k is the maximum complexity, $j = 1$ is a count of these covariates, and z_{tj} is the value of the j^{th} covariate at time point t , for example, the value of SST or NAO in a certain year (time point). Model fitting and candidate response count distributions are presented in Supplement 2. Within the GAMs themselves, the k parameter for storm events (count) in Model 1 was set to 7, to ensure enough flexibility in the model. k is the maximum complexity of the basis used to represent the respective smooth term, i.e. how many covariate combinations there are for that specific predictor. If the k value is high enough, we can be sure that there is enough flexibility in the model. We examined and refitted the model until k was high enough. To avoid fitting overly complex models the maximum basis size for the smooth terms was limited to these values (Wood 2011). The other variables (e.g. NAO_index) did not require an altered k parameter, since those terms had more unique covariate combinations than specified maximum degrees of freedom. We fitted models using restricted maximum likelihood (REML) in the R mgcv package version 1.8 -33 (Wood 2011). REML finds an optimal degree of smoothing for models with highly correlated covariates (Reiss & Todd Ogden 2009). As part of the model validation process, we made additional checks for model fit that looked at the per-covariate residuals (Fig. S1 in Supplement 2). Low variation in the covariate residuals suggests that the models are a good fit. We fitted models with the following candidate response count distributions: Poisson, quasi-Poisson, negative binomial, and Tweedie (Figs. S2 to S5 in Supplement 2).

3. RESULTS

3.1. Reported stranding data and potential drivers

Inter-annual variability in observed stranding numbers was high (0–26 ind. yr⁻¹) with the peak stranding event occurring in 2008 (Fig. 4). This was con-

firmed by GAM analyses, which showed a significant effect of year on observed numbers of turtles encountered in the UK in all models, i.e. across years (summarized in Table 2 and Fig. 5A). We found a significant effect ($p < 0.001$) of the NAO index, and weak effects of storm events over the North Atlantic (storm index, $p < 0.05$), UK SST ($p < 0.001$), and local storm events (storm count, $p < 0.01$) on stranding numbers (Model 1 in Table 2 and Fig. 5). The best model fit was the Poisson response count distribution (compare Figs. S2 to S5 in Supplement 2), with this model providing not only the best fit for the data but also the highest deviance explained (75.8%) (Table 2). Low p -values indicate that the smooth of that variable was significantly different from 'no effect' (if we estimated the smooth as a flat line at zero). The estimated degrees of freedom (EDF) for NAO (5.52) were highest (Model 1 in Table 2 and Fig. 5) showing a non-linear effect of NAO on stranding reports. The EDFs for North Atlantic storms (storm_index), local storms near the UK (storm_count) and local SST (mean_SST) were close to 1, which indicates a linear relationship (Model 1 in Table 2). We found no significant effects of the number of virtual turtles to arrive around the UK (simulated arrivals, Model 3 in Table 2), temperature-induced mortality rates (Model 3 in Table 2), the strength of northward GS transport or northward NAC transport (Model 2 in Table 2) on observed stranding numbers. Thus, using these specific models and this dataset and period, only NAO and local conditions explain the inter-annual vari-

ability in the observed numbers of turtles in the UK (Model 1 in Table 2). Summary plots of the model output for Model 2 are found in Fig. S6 and for Model 3 in Fig. S8 in Supplement 2. We validated that the oceanographic drivers in the GAMs are adequately selected by assessing their influence on virtual turtle arrival to the UK with a separate GAM, in which the drivers explain 93.8% of deviance (Table S1 in Supplement 1).

3.2. Fate of simulated hatchlings and drivers

Since simulated arrivals to the UK coast do not explain observed strandings, we demonstrate the oceanographic mechanisms that can lead to an increased abundance in UK waters. The numbers of virtual turtles simulated to arrive in the UK were modulated by GS northward transport, NAC northward transport, a yearly storm index obtained from atmospheric reanalysis, and NAO (Table 1 and Table S1 in Supplement 1). The decadal variability in virtual turtles simulated to arrive in the UK was linked to wind stress (the strength of westerly winds) across the North Atlantic (i.e. as indicated by storm_index) that drove eastward oceanic transport (Fig. 6). The magnitude of wind stress was mostly determined by the meridional sea level pressure pattern in the North Atlantic (NAO). In the ocean model simulations, virtual turtles either remained in the warm North Atlantic Gyre (not shown) or drifted with the North Atlantic Cur-

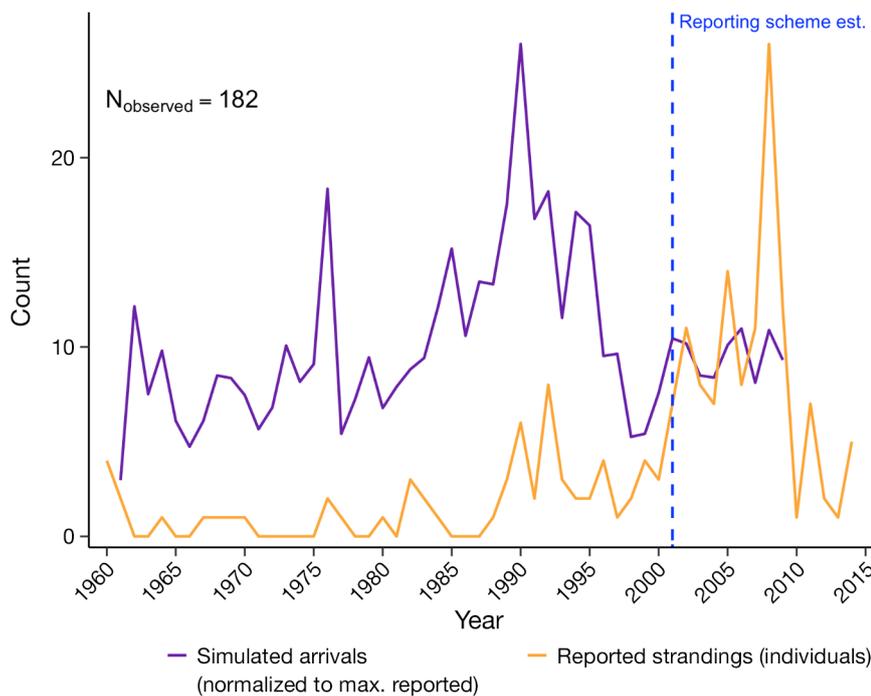


Fig. 4. Turtles arriving in the UK. Yearly stranding records of 182 juvenile sea turtles in the UK shown in orange (individuals recorded in database TURTLE; year of establishment indicated by blue dashed line); simulated arrivals of virtual turtles that reached the UK from the east coast of the USA in an ocean drift model shown in purple (count, normalized to maximum reported strandings to match scale, see Supplement 1, Text S2). Stranding records shown from 1960–2014 and simulated arrivals shown from 1961–2009 based on data availability

Table 2. Estimated degrees of freedom (EDFs) of covariates used to explain variability in observed strandings for the 3 generalized additive model analyses. Model 1 uses data from 1960–2014, Model 2 1960–2009, Model 3 1961–2007. s(): smooths of the covariates. Significant p-values (* $p < 0.05$, ** $p < 0.01$) show whether the smooth of that variable is significantly different from 'no effect', i.e. if we estimated the smooth as a flat line at zero. Modelled using the Poisson response count distribution

Covariates in model	EDF		
	Model 1	Model 2	Model 3
s(Storm_count)	0.95**		
s(Storm_index)	0.72*		
s(Mean_SST)	1.23**		
s(NAO_index)	5.52**		
s(NAC transport)		0.47	
s(GS transport)		<0.001	
s(Mortality)			<0.001
s(Simulated_arrivals)			0.56
s(Year)	1.12**	2.35**	1.28**

rent into cold waters (Fig. 2). Consistently low numbers of virtual turtles reached within 2 km of the UK coast after drifting northeast with the NAC, varying around a median of 0.83% (lower quartile 0.67%, upper quartile 1.02%). Median drift time was 635 d. Most virtual turtles that drifted to the UK or were exposed to cold temperature during the first year of drift, originated from release locations to the west (inshore) of the GS core (compare distribution of release positions between Panels A, B and C in Fig. S1 in Supplement 1). The estimated mortality resulting from exposure to 10 and 15°C was consistently low (median of 19% \pm 2.7 SD) across the ~5 decades of our study period (Fig. 2B). The median times at first exposure to 10 and 15°C were 185 and 150 d, respectively, with the majority (61%) of virtual turtles first experiencing these critical temperatures along the northerly boundary of the North Atlantic Gyre (~45° N, Fig. 2C,D).

4. DISCUSSION

4.1. Drivers of juvenile sea turtle strandings in the UK

This is the first study to investigate potential environmental drivers of sea turtle stranding events in the UK. We confirm that juvenile sea turtles from the coast of the USA can disperse to the UK under hazardous conditions (temperatures below 15 and 10°C) within the time expected based on the size of reported

strandings in relation to size at age curves reported (Bjørndal et al. 2000, Bolten 2003, Scott et al. 2012b). We show that variations in reported strandings of juvenile turtles in the UK are correlated with NAO phase, likely driven by westerly winds over the North Atlantic (indicated by the NAO index). We detect a small effect of storm events over the North Atlantic (offshore) but no effect of variable ocean currents (GS or NAC northward transport) using a GAM. Both storms and ocean currents are, however, indicated by NAO phase, and low numbers of reported juvenile strandings might inhibit our ability to detect an effect. We therefore use the drift model to demonstrate that NAO phase variation and related changes in wind-driven ocean current transport increase the supply of simulated juvenile turtles to the UK on decadal timescales. Because climatic indexes indicate an environmental mode, it can be useful to assess the influence of a set of environmental variates on ecological processes, particularly when the resolution of data does not allow us to disentangle the effects of singular variables and their complex interplay (Ottersen et al. 2001, Hurrell & Deser 2010). NAO phase reflects wind stress and storm track position across the North Atlantic (west to east), thus modulating ocean current transport and position, as well as SST (Ottersen et al. 2001, Visbeck et al. 2003). We demonstrate that this relationship holds true in our model and modulates virtual turtle transport to UK waters on decadal timescales.

While we found that numbers of turtles stranded in the UK were best explained by NAO, other studies found that recruitment to the Azores, a feeding habitat for Atlantic juvenile loggerhead turtles *Caretta caretta* southeast of the UK, is modulated by the number of nests at the source population in Florida, USA, in preceding years (Vandepierre et al. 2019, Putman et al. 2020) and not explained by stochastic events. In contrast, nest count numbers were not elevated before years with high stranding numbers in the UK in the years where data was available (since 1998; Ceriani et al. 2019). In fact, notably low nest counts during the early 2000s are followed by an all-time-high of reported strandings between 2000 and 2009 (Van Houtan & Halley 2011, Ceriani et al. 2019, present study). Our results indicate that dispersal at the edges of the species' distribution (as simulated here) might be more sensitive to environmental variability than along desirable warmer dispersal pathways in the North Atlantic (i.e. to developmental habitat around the Azores).

In addition to dispersion with currents, surface dwellers like juvenile sea turtles are sensitive to

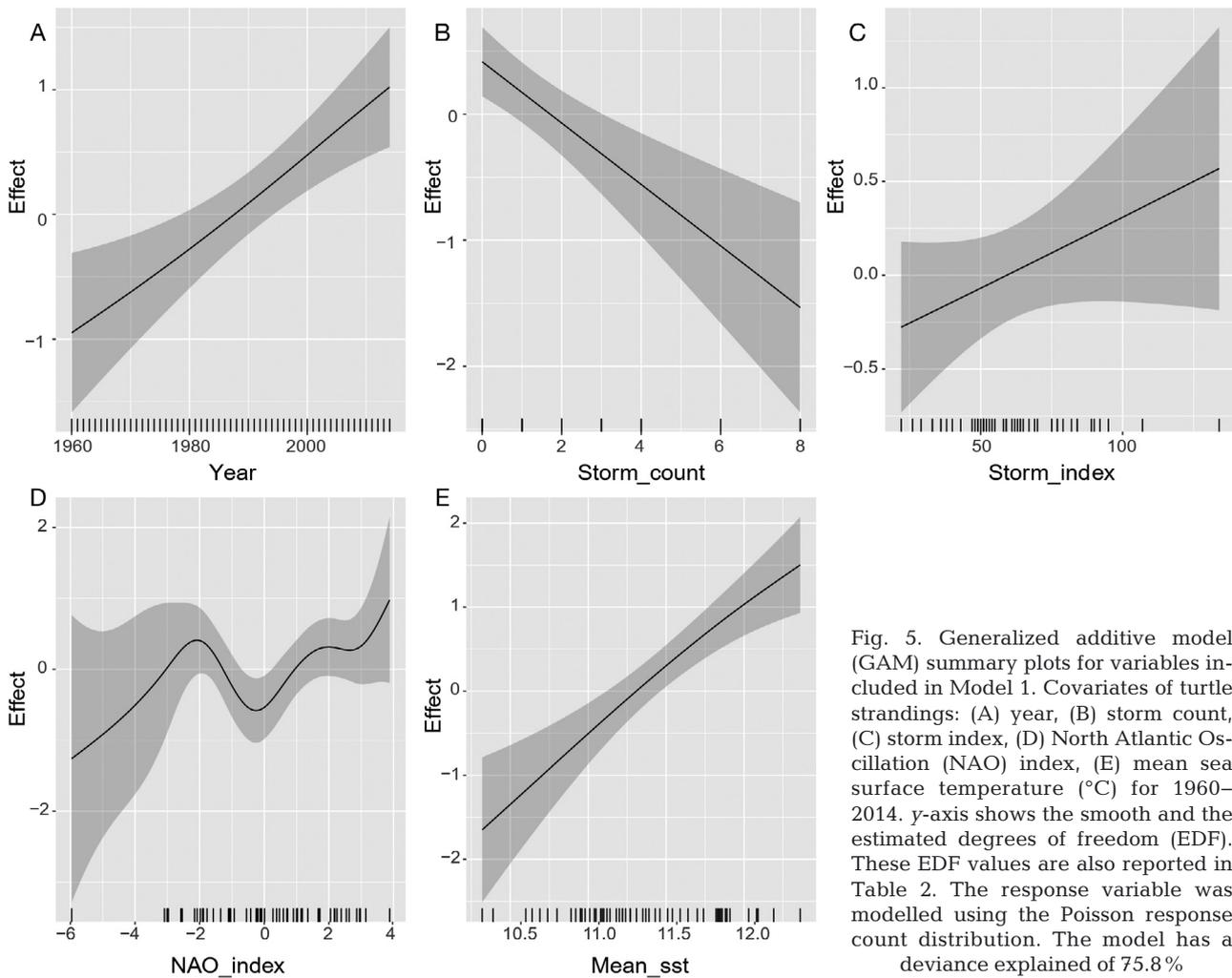


Fig. 5. Generalized additive model (GAM) summary plots for variables included in Model 1. Covariates of turtle strandings: (A) year, (B) storm count, (C) storm index, (D) North Atlantic Oscillation (NAO) index, (E) mean sea surface temperature ($^{\circ}\text{C}$) for 1960–2014. y-axis shows the smooth and the estimated degrees of freedom (EDF). These EDF values are also reported in Table 2. The response variable was modelled using the Poisson response count distribution. The model has a deviance explained of 75.8%

strong winds and can be displaced thousands of kilometers off course by storms (Monzón-Argüello et al. 2012, Waters et al. 2018). We found that storm events over the North Atlantic had a weak effect on reported strandings ('storm index', Table 2 Model 1). While primary wind effects are included in the ocean model forcing and simulated arrivals should thus reflect variability from storms across the North Atlantic, the lack of parametrization for secondary physical mechanism like 'Stokes drift', supplied by waves and swell, could be responsible for a model bias (Ardhuin et al. 2009, Curcic et al. 2016, Van Den Bremer & Breivik 2017). Future studies should thus use models parameterized to account for storm effects directly, i.e. representing displacement by Stokes' drift. Studies that actively tracked hatchlings during their first day at sea highlighted the influence of small-scale turbulence and wave/tide-induced motions (not represented or resolved by models) on turtle trajectories (Scott et al. 2014a). Nevertheless, due to the limita-

tions of active hatchling tracking studies, ocean models remain a valuable tool for studying ocean basin scale dispersion patterns with modelled drift simulations, and our results corroborate genetic studies linking juvenile turtles found at sea to natal nesting areas thousands of kilometers away (Monzón-Argüello et al. 2010, 2012).

We observe an increase in the number of juvenile turtles stranding in the UK over our study period. This could be partly attributed to an actual increase in turtles transported to the UK but can also be related to reporting effort, public interest, and the founding of marine environmental monitoring programs such as the TURTLE database in 2001 (see discussion in Botterell et al. 2020). Stranding numbers emerge from a complex interplay of abundance and mortality rate, as well as physical drivers on carcass drift (Hart et al. 2006, Santos et al. 2018, Cook et al. 2021) and observer effort (e.g. modulated by people at the coast, awareness), but we showcase that in-

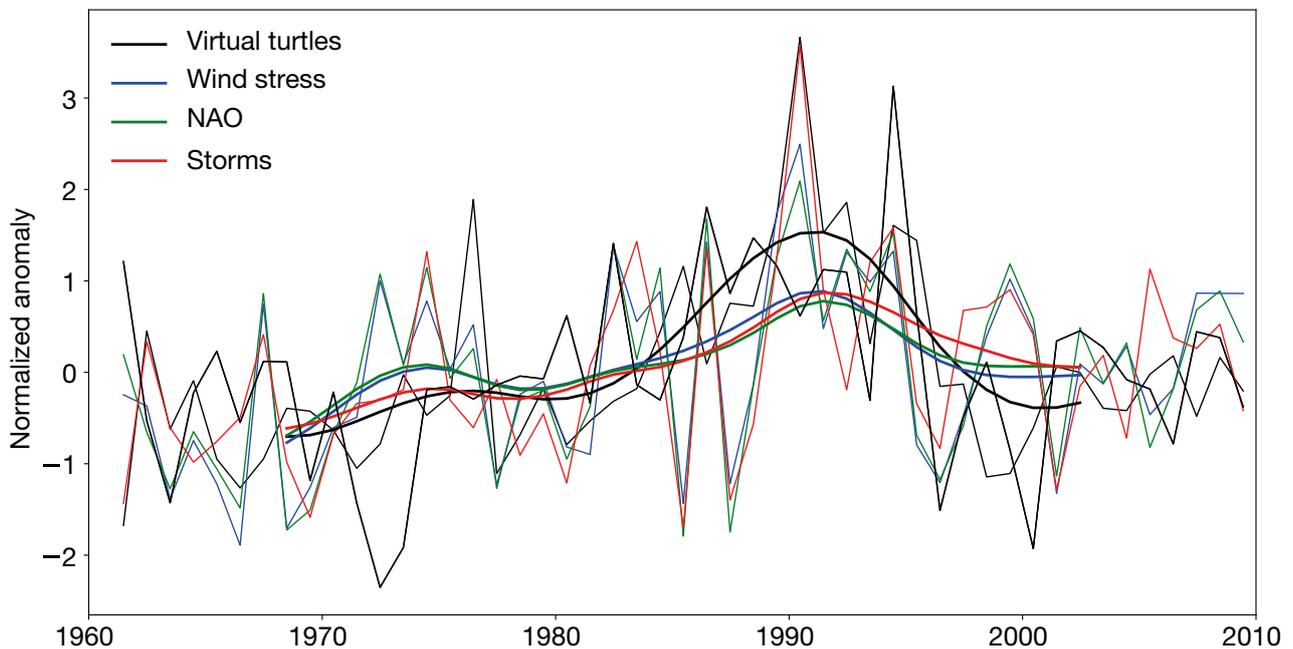


Fig. 6. Variability in wind stress, North Atlantic Oscillation (NAO) index and simulated arriving sea turtles in UK. Variability in simulated virtual turtles was linked with variability in the westerlies, the wind patterns which drive surface ocean currents eastward across the North Atlantic. Intensification of westerlies coincides with increased numbers of virtual turtles arriving in the UK. Wind stress is mostly determined by the meridional sea level pressure pattern in the North Atlantic, which is referred to as the NAO index. Data is shown from 1960–2009, when data from the ocean model was available with a 15 yr rolling average using a Hanning window. Thick lines are the smoothed time series (using the 15-yr Hanning window)

creased oceanic driven transport to waters surrounding the UK can mediate stranding numbers in addition to coastal circulation and weather effects. While we control for human population growth over the decades as a proxy for effort, smaller scale effects on observer effort are difficult to detect and require dedicated investigation (Hart et al. 2006, Coombs et al. 2019, Cook et al. 2021). We detected a weak positive effect of locally observed storms and mean SST around the UK on the number of reported juvenile turtles, variables also modulated by NAO phase (Visbeck et al. 2003). Our results indicate that juvenile turtles in UK waters are more likely to be detected in years with more local storms, perhaps stranded by stronger winds or brought closer to shore, where they are more likely to be detected during warmer years, reflected by the effect of local SST (Hart et al. 2006, Santos et al. 2018, Cook et al. 2021). These local effects on detectability might overpower underlying cause effects of long-distance dispersal signals that can lead to higher abundance in waters around the UK and thus inhibit our ability to detect an effect of ocean current transport on reported strandings directly in our GAMs (Hart et al. 2006, Santos et al. 2018, Cook et al. 2021). We lack the resolution to detect signals on a seasonal level because the strand-

ing data was compiled to yearly composite, as turtles are reported in various states of decomposition, making exact arrival times unavailable (see also discussion in Witt et al. 2006 and Botterell et al. 2020).

4.2. Mortality and dispersal patterns

We demonstrate that juvenile sea turtles can be advected out of the warm North Atlantic Gyre via the NAC, encountering lethally cold temperatures of 10°C during their first year of drift. We identified hazardous regions that turtles should avoid by mapping the locations in which virtual turtles first encountered lethal (10°C) or detrimental (15°C) temperatures. The most hazardous region, given the seasonal timing of hatching and drift pathways, is situated along the western edge of the GS. These regions coincide with magnetic field variations which elicit directed swimming in juvenile loggerhead turtles (Putman et al. 2012b). Our results suggest that temperature induced mortality rates are low (median of $19\% \pm 2.7$ SD) throughout the decades, in line with evidence from the Azores which suggests relatively stable recruitment when accounting for nesting numbers (Vandepierre et al. 2019). While stochastic events

can imperil young turtles, e.g. when they encounter eddies at the edge of the GS, these events might be avoided by active swimming, lowering the expected mortality rate further. Virtual turtles released west of the GS were more prone to experiencing cold temperatures, which underlines the importance of the initial 'swimming frenzy' which helps hatchlings escape predator-rich coastal waters and reach favorable offshore currents for transport to developmental habitats (Salmon & Wyneken 1987, Whelan & Wyneken 2007, Putman et al. 2012a). Future studies could use a subset of the available strandings data (e.g. the more recent years) to assess smaller scale effects and surface ocean processes such as Stoke's drift and their interactions on turtle strandings in Europe using local circulation models. Sensitivity analyses could also be performed to explore how active hatchling swimming behavior scenarios may prevent turtles from becoming cold-stunned and being advected along fatal drift trajectories to the UK.

Our model simulations show low variability in passive dispersion scenarios over the 5 decades of the study period (1960–2009) and consistently low temperature induced mortality. In contrast, variability in ocean-mediated dispersion can be high in other sea turtle nesting regions (Gaspar et al. 2012, Ascani et al. 2016, Scott et al. 2017) and has been linked to variation in recruitment of turtles and fish (Ruiz et al. 2013, Baltazar-Soares et al. 2014, Ascani et al. 2016). In the western North Atlantic, the success of nesting rookeries is linked to proximity to the GS, while in the Pacific, the variable position of another major ocean current modulates juvenile sea turtle survival and adult recruitment on decadal timescales (Putman et al. 2010, Ascani et al. 2016). In the North Atlantic, the stability of broadly favorable oceanic conditions encountered by juvenile sea turtles (evidenced by low simulated mortality rates) likely helps to ensure the population viability and success of the largest loggerhead sea turtle rookery reported in the world (Casale & Tucker 2015).

Sea turtle ecology is intimately linked to temperature regimes across their life cycle (Patrício et al. 2021). For example, increasing temperatures on nesting beaches affect the sex ratios of hatchlings and may render southern nesting regions non-viable (Hawkes et al. 2007); changes in SST can lead to changing spatial and seasonal distribution of turtles and their prey, impacting access to foraging habitats (Ascani et al. 2016) and causing range shifts (McMahon & Hays 2006). Since the dispersal routes of the juvenile life stages influence the migration behavior and distribution of adult sea turtles (Scott et al.

2014b), understanding the impacts of temperatures experienced during the juvenile dispersal stage is key to understanding how sea turtle populations will respond to a changing climate.

5. CONCLUSIONS

Our results suggest that environmental variability indicated by the NAO index is a driver of variability in sea turtle strandings in the UK since variations in westward wind stress drive ocean currents that transport turtles to the region. Stranding observations were only slightly correlated to storm frequency over the North Atlantic and not to temperature-induced mortality experienced during drift at the resolution of our model. Our model indicated that local factors such as coastal SST and storms had a small effect on stranding observations; turtles were more likely to be detected during years with local storms and high SST. Nevertheless, future studies should further investigate these mechanisms on shorter timescales which allow the use of higher resolution environmental data and more robust recent stranding reports. Furthermore, increased understanding of the sea turtle lost years is critical for conservation efforts (Bjorndal et al. 2003) since the population dynamics of marine species with dispersive juvenile stages can be modulated by survival rates of early life stages (Halley et al. 2018), which are susceptible to oscillations in climatic and oceanic factors (Baltazar-Soares et al. 2014). With anthropogenic climate change causing atmospheric and oceanic conditions to change, it is becoming ever more important to understand how organisms with drifting life stages will be affected by future environmental conditions.

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LITERATURE CITED

- ✦ Ardhuin F, Marié L, Rasclé N, Forget P, Roland A (2009) Observation and estimation of Lagrangian, Stokes, and Eulerian currents induced by wind and waves at the sea surface. *J Phys Oceanogr* 39:2820–2838
- ✦ Ascani F, Van Houtan KS, Di Lorenzo E, Polovina JJ, Jones TT (2016) Juvenile recruitment in loggerhead sea turtles linked to decadal changes in ocean circulation. *Glob Chang Biol* 22:3529–3538
- ✦ Baltazar-Soares M, Biastoch A, Harrod C, Hanel R and others (2014) Recruitment collapse and population structure of the European eel shaped by local ocean current dynamics. *Curr Biol* 24:104–108
- ✦ Barnier B, Madec G, Penduff T, Molines JM and others (2006) Impact of partial steps and momentum advection schemes in a global ocean circulation model at eddy-permitting resolution. *Ocean Dyn* 56:543–567
- Behrens E (2013) The oceanic response to Greenland melting: the effect of increasing model resolution. PhD thesis, Christian-Albrechts-Universität zu Kiel
- ✦ Bjorndal KA, Bolten AB, Martins HR (2000) Somatic growth model of juvenile loggerhead sea turtles *Caretta caretta*: duration of pelagic stage. *Mar Ecol Prog Ser* 202:265–272
- Bjorndal KA, Bolten AB, Martins HR (2003) Estimates of survival probabilities for oceanic-stage loggerhead sea turtles (*Caretta caretta*) in the North Atlantic. *Fish Bull* 101: 732–736
- ✦ Blanke B, Arhan M, Madec G, Roche S (1999) Warm water paths in the equatorial Atlantic as diagnosed with a general circulation model. *J Phys Oceanogr* 29:2753–2768
- ✦ Blumenthal JM, Abreu-Grobois FA, Austin TJ, Broderick AC and others (2009) Turtle groups or turtle soup: dispersal patterns of hawksbill turtles in the Caribbean. *Mol Ecol* 18:4841–4853
- Bolten AB (2003) Variation in sea turtle life history patterns: neritic vs. oceanic developmental stages. In: Lutz P, Musick JA, Wyneken J (eds) *The biology of sea turtles*, Vol II. CRC Press, Boca Raton, FL, p 243–257
- ✦ Bolten AB, Bjorndal KA, Martins HR, Dellinger T, Bischoff MJ, Encalada SE, Bowen BW (1998) Transatlantic developmental migrations of loggerhead sea turtles demonstrated by mtDNA sequence analysis. *Ecol Appl* 8:1–7
- ✦ Böning CW, Behrens E, Biastoch A, Getzlaff K, Bamber JL (2016) Emerging impact of Greenland meltwater on deepwater formation in the North Atlantic Ocean. *Nat Geosci* 9:523–527
- ✦ Botterell ZLR, Penrose R, Witt MJ, Godley BJ (2020) Long-term insights into marine turtle sightings, strandings and captures around the UK and Ireland (1910–2018). *J Mar Biol Assoc UK* 100:869–877
- ✦ Boyle MC, FitzSimmons NN, Limpus CJ, Kelez S, Velez-Zuazo X, Waycott M (2009) Evidence for transoceanic migrations by loggerhead sea turtles in the southern Pacific Ocean. *Proc R Soc B* 276:1993–1999
- ✦ Breckenfelder T, Rhein M, Roessler A, Böning CW, Biastoch A, Behrens E, Mertens C (2017) Flow paths and variability of the North Atlantic Current: a comparison of observations and a high-resolution model. *J Geophys Res Ocean* 122:2686–2708
- ✦ Breusing C, Biastoch A, Drews A, Metaxas A and others (2016) Biophysical and population genetic models predict the presence of ‘phantom’ stepping stones connecting Mid-Atlantic Ridge vent ecosystems. *Curr Biol* 26: 2257–2267
- Brongersma LD (1972) European Atlantic turtles. *Zool Verh* 121:1–318
- Carr A (1952) *Handbook of turtles: the turtles of the United States, Canada and Baja California*. Cornell University Press, NY
- ✦ Casale P, Tucker AD (2015) *Caretta caretta*. The IUCN Red List of Threatened Species 2015 (accessed 2 March 2016) doi:10.2305/IUCN.UK.2015-4.RLTS.T3897A83157651.en
- ✦ Ceriani SA, Casale P, Brost M, Leone EH, Witherington BE (2019) Conservation implications of sea turtle nesting trends: elusive recovery of a globally important loggerhead population. *Ecosphere* 10:e02936
- ✦ Chapman JW, Nesbit RL, Burgin LE, Reynolds DR, Smith AD, Middleton DR, Hill JK (2010) Flight orientation behaviors promote optimal migration trajectories in high-flying insects. *Science* 327:682–685
- ✦ Cook M, Reneker JL, Nero RW, Stacy BA, Hanisko DS, Wang Z (2021) Use of drift studies to understand seasonal variability in sea turtle stranding patterns in Mississippi. *Front Mar Sci* 8:1–17
- ✦ Coombs EJ, Deaville R, Sabin RC, Allan L and others (2019) What can cetacean stranding records tell us? A study of UK and Irish cetacean diversity over the past 100 years. *Mar Mamm Sci* 35:1527–1555
- ✦ Curcic M, Chen SS, Özgökmen TM (2016) Hurricane-induced ocean waves and Stokes drift and their impacts on surface transport and dispersion in the Gulf of Mexico. *Geophys Res Lett* 43:2773–2781
- Davenport J, De Verteuil N, Magill SH (1997) The effects of current velocity and temperature upon swimming in juvenile green turtles *Chelonia mydas* L. *Herpetol J* 7: 143–147
- ✦ Debreu L, Vouland C, Blayo E (2008) AGRIF: adaptive grid refinement in Fortran. *Comput Geosci* 34:8–13
- ✦ Fichet T, Maqueda MAM (1997) Sensitivity of a global sea ice model to the treatment of ice thermodynamics and dynamics. *J Geophys Res Oceans* 102:12609–12646
- ✦ Fisher R, Leis JM, Clark DL, Wilson SK (2005) Critical swimming speeds of late-stage coral reef fish larvae: variation within species, among species and between locations. *Mar Biol* 147:1201–1212
- ✦ Fuxjager MJ, Eastwood BS, Lohmann KJ (2011) Orientation of hatchling loggerhead sea turtles to regional magnetic fields along a transoceanic migratory pathway. *J Exp Biol* 214:2504–2508
- ✦ Gaspar P, Benson SR, Dutton PH, Réveillère A and others (2012) Oceanic dispersal of juvenile leatherback turtles: going beyond passive drift modeling. *Mar Ecol Prog Ser* 457:265–284
- ✦ Griffies SM, Biastoch A, Böning C, Bryan F and others (2009) Coordinated ocean-ice reference experiments (COREs). *Ocean Model* 26:1–46
- ✦ Guisan A, Edwards TC Jr, Hastie T (2002) Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecol Modell* 157:89–100
- ✦ Halley JM, Van Houtan KS, Mantua N (2018) How survival curves affect populations’ vulnerability to climate change. *PLOS ONE* 13:e0203124
- ✦ Hart KM, Mooreside P, Crowder LB (2006) Interpreting the spatio-temporal patterns of sea turtle strandings: going with the flow. *Biol Conserv* 129:283–290
- ✦ Hawkes LA, Broderick AC, Coyne MS, Godfrey MH, Godley BJ (2007) Only some like it hot—quantifying the environmental niche of the loggerhead sea turtle. *Divers Distrib* 13:447–457

- Hurrell JW, Deser C (2010) North Atlantic climate variability: the role of the North Atlantic Oscillation. *J Mar Syst* 79:231–244
- Kinlan BP, Gaines SD (2003) Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology* 84:2007–2020
- LaCasella EL, Epperly SP, Jensen MP, Stokes L, Dutton PH (2013) Genetic stock composition of loggerhead turtles *Caretta caretta* bycaught in the pelagic waters of the North Atlantic. *Endang Species Res* 22:73–84
- Lamb H, Frydendahl K (1991) *Historic storms of the North Sea, British Isles and Northwest Europe*. Cambridge University Press, Cambridge
- Large WG, Yeager SG (2008) The global climatology of an interannually varying air–sea flux data set. *Clim Dyn* 33:341–364
- Levitus S, Boyer TP, Conkright ME, O'brien T and others (1998) NOAA Atlas NESDIS 18, World Ocean Database 1998, Vol 1, Introduction. US Government Printing Office Washington, DC, p 1–3
- Lohmann KJ, Lohmann CMF, Endres CS (2008) The sensory ecology of ocean navigation. *J Exp Biol* 211:1719–1728
- Maldini D, Mazzuca L, Atkinson S (2005) Odontocete stranding patterns in the main Hawaiian Islands (1937–2002): How do they compare with live animal surveys? 1. *Pac Sci* 59:55–67
- Marra G, Wood SN (2011) Practical variable selection for generalized additive models. *Comput Stat Data Anal* 55:2372–2387
- McMahon CR, Hays GC (2006) Thermal niche, large-scale movements and implications of climate change for a critically endangered marine vertebrate. *Glob Chang Biol* 12:1330–1338
- Meinen CSC, Baringer MO, Garcia RFR (2010) Florida Current transport variability: an analysis of annual and longer-period signals. *Deep Sea Res I* 57:835–846
- Milsom WK (1975) Development of buoyancy control in juvenile Atlantic loggerhead turtles, *Caretta c. caretta*. *Copeia* 1975:758–762
- Monzón-Argüello C, Rico C, Carreras C, Calabuig P, Marco A, López-Jurado LF (2009) Variation in spatial distribution of juvenile loggerhead turtles in the eastern Atlantic and western Mediterranean Sea. *J Exp Mar Biol Ecol* 373:79–86
- Monzón-Argüello C, López-Jurado LF, Rico C, Marco A, López P, Hays GC, Lee PLM (2010) Evidence from genetic and Lagrangian drifter data for transatlantic transport of small juvenile green turtles. *J Biogeogr* 37:1752–1766
- Monzón-Argüello C, Dell'Amico F, Morinière P, Marco A and others (2012) Lost at sea: genetic, oceanographic and meteorological evidence for storm-forced dispersal. *J R Soc Interface* 9:1725–1732
- Murphy T, Hopkins S (1984) Aerial and ground surveys of marine turtle nesting beaches in the southeast region, US. United States Final Report to NMFS_SEFSC, Miami: 73
- North EW, Schlag Z, Hood RR, Li M, Zhong L, Gross T, Kennedy VS (2008) Vertical swimming behavior influences the dispersal of simulated oyster larvae in a coupled particle-tracking and hydrodynamic model of Chesapeake Bay. *Mar Ecol Prog Ser* 359:99–115
- Ottersen G, Planque B, Belgrano A, Post E, Reid PC, Stenseth NC (2001) Ecological effects of the North Atlantic Oscillation. *Oecologia* 128:1–14
- Patrício AR, Hawkes LA, Monsinjon JR, Godley BJ, Fuentes MMPB (2021) Climate change and marine turtles: recent advances and future directions. *Endang Species Res* 44:363–395
- Penhallurick RD (1990) *Turtles off Cornwall, The Isles of Scilly and Devonshire*. Dyllansow Pengwella, Truro
- Putman NF, Naro-Maciel E (2013) Finding the 'lost years' in green turtles: insights from ocean circulation models and genetic analysis. *Proc Biol Sci* 280:20131468
- Putman NF, Bane JM, Lohmann KJ (2010) Sea turtle nesting distributions and oceanographic constraints on hatchling migration. *Proc R Soc B Biol Sci* 277:3631–3637
- Putman NF, Scott R, Verley P, Marsh R, Hays GC (2012a) Natal site and offshore swimming influence fitness and long-distance ocean transport in young sea turtles. *Mar Biol* 159:2117–2126
- Putman NF, Verley P, Shay TJ, Lohmann KJ (2012b) Simulating transoceanic migrations of young loggerhead sea turtles: merging magnetic navigation behavior with an ocean circulation model. *J Exp Biol* 215:1863–1870
- Putman NF, Seney EE, Verley P, Shaver DJ, López-Castro MC, Cook M, Guzmán V and others (2020) Predicted distributions and abundances of the sea turtle 'lost years' in the western North Atlantic Ocean. *Ecography* 43:506–517
- Pyenson ND (2011) The high fidelity of the cetacean stranding record: insights into measuring diversity by integrating taphonomy and macroecology. *Proc R Soc B* 278:3608–3616
- Reiss PT, Todd Ogden R (2009) Smoothing parameter selection for a class of semiparametric linear models. *J R Stat Soc B Stat Methodol* 71:505–523
- Richardson PL (1985) Average velocity and transport of the Gulf Stream near 55W. *J Mar Res* 43:83–111
- Ruiz J, Macías D, Rincón MM, Pascual A, Catalán IA, Navarro G (2013) Recruiting at the edge: kinetic energy inhibits anchovy populations in the western Mediterranean. *PLOS ONE* 8:e55523
- Salmon M, Wynneken J (1987) Orientation and swimming behavior of hatchling loggerhead turtles *Caretta caretta* L. during their offshore migration. *J Exp Mar Biol Ecol* 109:137–153
- Santos BS, Friedrichs MAM, Rose SA, Barco SG, Kaplan DM (2018) Likely locations of sea turtle stranding mortality using experimentally-calibrated, time and space-specific drift models. *Biol Conserv* 226:127–143
- Schwartz FJ (1976) Behaviour and tolerance responses to cold water temperatures by three species of sea turtles (reptilia, cheloniidae) in North Carolina. *Fla Mar Res Publ* 33:40607–40609
- Scott R, Marsh R, Hays GC (2012a) A little movement orientated to the geomagnetic field makes a big difference in strong flows. *Mar Biol* 159:481–488
- Scott R, Marsh R, Hays GC (2012b) Life in the really slow lane: loggerhead sea turtles mature late relative to other reptiles. *Funct Ecol* 26:227–235
- Scott R, Biastoch A, Roder C, Stiebens VA, Eizaguirre C (2014a) Nano-tags for neonates and ocean-mediated swimming behaviours linked to rapid dispersal of hatchling sea turtles. *Proc R Soc B* 281:1796
- Scott R, Marsh R, Hays GC (2014b) Ontogeny of long distance migration. *Ecology* 95:2840–2850
- Scott R, Biastoch A, Agamboue PD, Bayer T and others (2017) Spatio-temporal variation in ocean current-driven hatchling dispersion: implications for the world's largest leatherback sea turtle nesting region. *Divers Distrib* 23:604–614

- ✦ Siegel DA, Kinlan BP, Gaylord B, Gaines SD (2003) Lagrangian descriptions of marine larval dispersion. *Mar Ecol Prog Ser* 260:83–96
- ✦ Tsujino H, Urakawa S, Nakano H, Small RJ and others (2018) JRA-55 based surface dataset for driving ocean–sea-ice models (JRA55-do). *Ocean Model* 130:79–139
- ✦ van den Bremer TS, Breivik Ø (2017) Stokes drift. *Philos Trans R Soc A Math Phys Eng Sci* 376:20170104
- ✦ Van Houtan KS, Halley JM (2011) Long-term climate forcing in loggerhead sea turtle nesting. *PLOS ONE* 6:e19043
- ✦ Vandeperre F, Parra H, Pham CK, Machete M, Santos M, Bjørndal KA, Bolten AB (2019) Relative abundance of oceanic juvenile loggerhead sea turtles in relation to nest production at source rookeries: implications for recruitment dynamics. *Sci Rep* 9:13019
- ✦ Visbeck M, Chassignet EP, Curry RG, Delworth TL, Dickson RR, Krahnmann G (2003) 6. The ocean's response to North Atlantic oscillation variability. *Atlantic* 15:2581–2597
- ✦ Waters JM, King TM, Fraser CI, Craw D (2018) Crossing the front: contrasting storm-forced dispersal dynamics revealed by biological, geological and genetic analysis of beach-cast kelp. *J R Soc Interface* 15: 20180046
- ✦ Whelan CL, Wyneken J (2007) Estimating predation levels and site-specific survival of hatchling loggerhead sea turtles (*Caretta caretta*) from south Florida beaches. *Copeia* 2007:745–754
- ✦ Witt MJ, Penrose R, Godley BJ (2006) Spatio-temporal patterns of juvenile marine turtle occurrence in waters of the European continental shelf. *Mar Biol* 151:873–885
- ✦ Wood SN (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J R Stat Soc B Stat Methodol* 73:3–36
- ✦ Wyneken J, Salmon M (1992) Frenzy and postfrenzy swimming activity in loggerhead, green, and leatherback hatchling sea turtles. *Copeia* 1992:478
- ✦ Wyneken J, Madrak SV, Salmon M, Foote J (2008) Migratory activity by hatchling loggerhead sea turtles (*Caretta caretta* L.): evidence for divergence between nesting groups. *Mar Biol* 156:171–178

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