Article

A Global Assessment of the Potential for Ocean-Driven Transport in Hatchling Sea Turtles

Morgan J. DuBois ^{1,*}, Nathan F. Putman ² and Susan E. Piacenza ¹ ¹ Biology Department, The University of West Florida, Pensacola, FL 32514, USA; spiacenza@uwf.edu² LGL Ecological Research Associates, Bryan, TX 77802, USA; nathan.putman@gmail.com

* Correspondence: mjdubois01@gmail.com

Abstract: Ocean circulation models are an essential tool for use in estimating the movements of drifting marine species. Across the world, hatchling sea turtle transport to the pelagic ocean is facilitated by the local currents off their natal beaches. It is difficult, if not impossible, to observe this transport reliably for any lengthy period, and, as such, ocean circulation models are an essential tool for studying sea turtles during this vulnerable time. Here, we use the ocean circulation model HYCOM and the particle simulator Ichthyop to model the first month of hatchling transport across all sea turtle species from nesting sites across the world from 25 cohorts of hatchlings at 67 nesting sites. We evaluated transport as a function of spatiotemporal factors that could influence turtle movement, using generalized linear models and the information theoretic approach to model selection. We found that multiple physical factors influence transport across the first month of movement and that annual variability is an important factor in hatchling transport. Our findings suggest that the beaches turtles hatch from and the year in which they hatch may shape their early life and the speed of transport into the relative safety of the open ocean. An increased understanding of the likely survival of a cohort may aid in designating funds and planning conservation strategies for individual beaches to either compensate for or take advantage of the local currents.

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1. Introduction

Ocean currents play an important role in the spatial distribution of many marine plants, invertebrates, and vertebrates as the main driver of movement, ontogenetic shifts in habitats, and dispersal in individual organisms [1]. At a population level, the importance of ocean currents is readily apparent in the timing of reproduction, the location of reproductive sites [1–3], and spatiotemporal variation in recruitment dynamics [4]. On longer timescales, ocean currents shape the magnitude and directionality of gene flow among populations, colonization, and speciation [5,6]. Indeed, a reasonable null-hypothesis for ecological patterns and evolutionary processes in marine environments is that they are driven entirely by ocean circulation dynamics [7–9]. Global ocean circulation models have become valuable tools for generating the predictions of that null hypothesis, by providing a realistic environment within which the movements of individual organisms can be simulated [10]. Here, we use this framework to quantify differences in the potential ocean-driven transport of hatchling sea turtles departing nesting beaches.

Like many marine taxa, the sea turtle life cycle is characterized by movement [11]. Sea turtles deposit nests on warm, sandy beaches where eggs incubate for a period of weeks. When sea turtles hatch, they exhibit intense swimming behavior, dubbed the “swimming frenzy”, lasting 12 to 48 h that helps them quickly leave the continental shelf [2,12–14]. Nearshore predation is high for hatchlings, and they are less likely to be found and eaten in the open ocean than they are in the relatively shallow water of the continental shelf [15–17]. The young turtles of most species remain in open ocean habitats for several

years, carried by prevailing ocean currents and, in at least some cases, following an innate migratory route to distant, productive foraging grounds [18,19]. As turtles grow, some species move to more coastal habitats, whereas others remain in the open sea. Upon reaching maturity, there is a strong propensity for all species to return to the vicinity of their natal site to mate and nest [2,20,21]. This “natal homing” behavior is an important aspect for maintaining population structure and promoting demographic independence among nesting assemblages, despite the potential for widespread mixing in the oceanic habitats they occupy [22].

There is accumulating evidence that the hatchling migration is a critical period in the sea turtle life cycle. Observed hatchling mortality during this period ranges from 0–85% and likely depends upon beach conditions, predator density, geography of the beach and nearby ocean currents [15–17]. Consistent differences among nesting sites in how ocean currents facilitate the transport of hatchlings offshore may be a determining factor in regional variation in population sizes [11]. This period of oceanic transport also contributes to the distribution of juvenile turtles [10,23] and, possibly, the subsequent selection of foraging grounds by adults [24,25]. Given that this relatively brief period of the sea turtle life cycle has implications ranging from explaining biogeographic patterns of nest densities [26] to better managing fisheries [27], we investigated spatiotemporal variability in the oceanic transport of sea turtle hatchlings from 67 nesting beaches scattered across the globe. We used 25 years of hindcast ocean circulation model output paired with virtual particle tracking software to simulate the ocean-driven transport of non-swimming hatchling sea turtles. In addition to examining variability in transport potential among sites and through time, we evaluated whether these differences revealed any broad-scale trends of transport as a function of ocean basin, latitude, longitude, or coastal setting.

2. Methods

2.1. Particle Tracking Simulation

In our transportation simulations, we used the Global Hybrid Coordinate Ocean Model (HYCOM) to provide hindcast oceanic current conditions [28]. HYCOM provides a model environment of ocean current features at 0.08° resolution (~8–9 km grid spacing at mid-latitudes) and daily timesteps by integrating in situ and satellite data. We used the surface layer (~0–1 m) from experiments 19.0, 19.1, 91.0, 91.1, and 91.2 for the years 1993 to 2017 to provide background conditions for our particle simulation (<https://www.hycom.org/>).

Using Ichthyop (v. 2 Ichthyop, Lyons, France) particle tracking software, we simulated transportation from the selected nesting sites [29]. Ichthyop uses a Runge-Kutta 4th-order time step method to simulate the movement of virtual particles in ocean circulation model velocity fields. To better match how turtles behave in reality, we used a “bouncy” coastline, so that particles would move along or bounce off the coast rather than be stranded on shore and removed from the simulation. We released 350 particles day^{−1} during the typical hatching season for each site from 1993 to 2017. The model tracked the location and path of the particles for 30 days post release.

We measured the transport distance (km) of the turtles from their nesting beaches at 4 specific periods, 1, 5, 10, and 30 day(s) using the positions recorded from Ichthyop and functions in Python (v. 2.2 Python Software Foundation, Wilmington, DE, USA). We selected the first month of transport to examine short-term transport as turtles are at their smallest and most vulnerable during that period and rapid movement away from the shelf habitat is critical [15–17]. While swimming by sea turtles at this stage can have important implications for movements, distribution, and survival [14,30,31], we did not consider it here as our aim was only to examine the environmental setting into which turtles dispersed rather than the direct behavior of hatchling turtles. Distance was recorded as the straight (rhumb) line distance between the initial particle location and its position at a given timestep. From the simulated distances at each site, we calculated the standard deviation to estimate the variability of transport distance.

2.2. Nesting Beach Selection

We simulated short term transport of hatchling sea turtles from 67 sites around the world (Figure 1). We chose sites that represented a diversity of countries and ocean regions including the Atlantic Ocean, the Pacific Ocean, the Indian Ocean, the Mediterranean Sea, the Caribbean Sea, and the Red Sea (Tables 1 and A1 see Appendix A). Each of the seven species of turtles are represented by ≥ 3 sites and several sites represented multiple species. The loggerhead sea turtle, *Caretta caretta*, was represented by 28 sites, green sea turtle, *Chelonia mydas*, was represented by 24 sites, hawksbill sea turtle, *Eretmochelys imbricata*, by 15, leatherback sea turtle, *Dermochelys coriacea*, by 13, olive ridley sea turtle, *Lepidochelys olivacea* by 9, and Kemp's ridley sea turtle, *Lepidochelys kempii*, and Flatback sea turtle, *Natator depressus*, by 3 sites each. The differing site representation is due to the relative numbers of nesting sites for each species globally. For each site, we chose a single point to represent the nesting area location (i.e., latitude and longitude). We also categorized the ocean region the site is located within and the type of coast (i.e., shallow islands, deep islands, or continental coasts).

Figure 1. Global map of simulated sea turtle nesting sites with 5-day mean surface current velocities (m/s) from the Global Hybrid Coordinate Ocean Model from 2015.

Table 1. Nesting beach sites included in the study, organized alphabetically by Ocean Region and then by country. Each site is listed with the ocean region and coast type assigned to it for this study as well as the species found at the site and the mean transport distance (km) at the thirty-day interval with the standard deviation.

Ocean Region	Site	Coast Type	Species	Mean Distance (km) $\pm$ SD
Caribbean	Long Island, Antigua	Shallow Island	Hawksbill	357.26 $\pm$ 162.58
Caribbean	Tortola, British Virgin Islands	Shallow Island	Leatherback	348.04 $\pm$ 162.91
Caribbean	Klein Bonaire Beaches, Caribbean Netherlands	Shallow Island	Hawksbill, Loggerhead, Green	784.21 $\pm$ 341.47
Caribbean	Cahuita National Park, Costa Rica	Coastal	Hawksbill, Leatherback	127.48 $\pm$ 49.43
Caribbean	Grandoca, Costa Rica	Coastal	Hawksbill, Green, Leatherback	314.29 $\pm$ 209.04
Caribbean	Tortuguero, Costa Rica	Coastal	Green, Leatherback	209.64 $\pm$ 62.27
Caribbean	Culebra Island, Puerto Rico	Shallow Island	Leatherback	153.39 $\pm$ 112.07

Table 1. Cont.

Ocean Region	Site	Coast Type	Species	Mean Distance (km) $\pm$ SD
Caribbean	Fajardo-Luquillo, Puerto Rico	Shallow Island	Leatherback	405.42 $\pm$ 157.01
Caribbean	St. Croix National Wildlife Refuge, US Virgin Islands	Shallow Island	Leatherback	255.34 $\pm$ 132.54
Eastern Pacific	Ostional, Costa Rica	Coastal	Olive Ridley	640.17 $\pm$ 373.76
Eastern Pacific	Galapagos Islands, Ecuador	Deep Island	Green	817.57 $\pm$ 254.52
Eastern Pacific	Chiriqui, Panama	Coastal	Hawksbill, Leatherback	67.22 $\pm$ 64.66
Gulf of Mexico	Dry Tortugas-Loggerhead Key, US Florida	Coastal	Loggerhead	542.06 $\pm$ 376.87
Gulf of Mexico	Gulf Islands National Sea Shore, US Florida	Coastal	Loggerhead	117.80 $\pm$ 84.26
Gulf of Mexico	Siesta Key, US Florida	Coastal	Loggerhead	109.51 $\pm$ 69.32
Gulf of Mexico	Campeche, Mexico	Coastal	Hawksbill, Green	198.10 $\pm$ 58.90
Gulf of Mexico	Rancho Nuevo, Mexico	Coastal	Kemp's Ridley	208.76 $\pm$ 105.57
Gulf of Mexico	Veracruz, Mexico	Coastal	Kemp's Ridley	169.55 $\pm$ 77.40
Gulf of Mexico	Padre Island, US Texas	Coastal	Kemp's Ridley	68.73 $\pm$ 34.26
Indian Ocean	Cable Beach, Australia	Coastal	Flatback	165.59 $\pm$ 92.52
Indian Ocean	Gnaraloo Bay, Australia	Coastal	Loggerhead, Green	383.30 $\pm$ 131.90
Indian Ocean	Ningaloo, Australia	Coastal	Hawksbill, Loggerhead, Green	366.13 $\pm$ 133.52
Indian Ocean	Peak Island, Australia	Shallow Island	Flatback	342.37 $\pm$ 148.40
Indian Ocean	Europa Island, French Southern Territories	Deep Island	Green	408.04 $\pm$ 202.57
Indian Ocean	Glorieuses Island, French Southern Territories	Deep Island	Green	570.20 $\pm$ 246.75
Indian Ocean	Tromelin Island, French Southern Territories	Deep Island	Green	448.90 $\pm$ 216.00
Indian Ocean	Gahirmatha, India	Coastal	Olive Ridley	283.97 $\pm$ 89.57
Indian Ocean	Mayotte, Mayotte	Deep Island	Green	401.27 $\pm$ 213.02
Indian Ocean	Ponta do Ouro, Mozambique	Coastal	Loggerhead, Leatherback	580.24 $\pm$ 325.16
Indian Ocean	Karachi, Pakistan	Coastal	Green, Olive Ridley	126.48 $\pm$ 71.53
Indian Ocean	Silhouette Island, Seychelles	Shallow Island	Hawksbill	679.59 $\pm$ 400.10
Mediterranean	Kyparissa Town, Greece	Coastal	Loggerhead	198.85 $\pm$ 82.50
Mediterranean	Zakynthos, Greece	Shallow Island	Loggerhead	205.12 $\pm$ 90.45
Mediterranean	El Mansouri, Lebanon	Coastal	Loggerhead, Green	244.07 $\pm$ 86.81
Mediterranean	Kurait, Tunisia	Shallow Island	Loggerhead	134.64 $\pm$ 62.72
Mediterranean	Dalyan Beach, Turkey	Coastal	Loggerhead	267.44 $\pm$ 111.22
Mediterranean	Fethiye Beach, Turkey	Coastal	Loggerhead	267.36 $\pm$ 98.54

Table 1. Cont.

Ocean Region	Site	Coast Type	Species	Mean Distance (km) $\pm$ SD
Mediterranean	Goksu Delta, Turkey	Coastal	Loggerhead	263.90 $\pm$ 112.62
Mediterranean	Patara Beach, Turkey	Coastal	Loggerhead	264.93 $\pm$ 103.56
North Atlantic	Archie Carr National Wildlife Refuge, US Florida	Coastal	Green	228.08 $\pm$ 196.90
North Atlantic	Amelia Island, US Florida	Coastal	Loggerhead	119.91 $\pm$ 94.11
North Atlantic	Canaveral Air Force Station, US Florida	Coastal	Loggerhead	329.44 $\pm$ 295.21
North Atlantic	Wassaw, US Georgia	Coastal	Loggerhead	189.37 $\pm$ 117.13
North Atlantic	Bald Head Island, US North Carolina	Coastal	Loggerhead	331.15 $\pm$ 235.88
North Atlantic	Huntington Beach State Park, US South Carolina	Coastal	Loggerhead	204.72 $\pm$ 139.22
North Atlantic	Hunting Island SP, US South Carolina	Coastal	Loggerhead	157.79 $\pm$ 90.37
North Pacific	French Frigate Shoals, US Hawaii	Deep Island	Green	361.83 $\pm$ 149.02
Northern Pacific	Miyazaki, Japan	Coastal	Loggerhead	305.24 $\pm$ 222.95
Red Sea	Jazā'ir Jiftūn, Egypt	Shallow Island	Hawksbill	224.84 $\pm$ 133.89
Red Sea	Wadi el Gemal, Egypt	Coastal	Green	186.37 $\pm$
Red Sea	Zabargad, Egypt	Shallow Island	Green	74.67 $\pm$ 48.07
South Atlantic	Ascension Island	Deep Island	Green	452.39 $\pm$ 159.76
South Atlantic	Bahia, Brazil	Coastal	Hawksbill, Loggerhead, Olive Ridley	154.17 $\pm$ 131.20
South Atlantic	Espirito Santo, Brazil	Coastal	Loggerhead, Leatherback	79.19 $\pm$ 79.14
South Atlantic	Congo Coast, Congo	Coastal	Olive Ridley, Leatherback	440.48 $\pm$ 189.94
South Atlantic	Bioko Island, Guinea	Shallow Island	Hawksbill, Green, Loggerhead, Leatherback	115.91 $\pm$ 14.96
Western Pacific	Heron Island, Australia	Shallow Island	Loggerhead, Green	336.78 $\pm$ 142.45
Western Pacific	Milman Island, Australia	Shallow Island	Hawksbill	314.12 $\pm$ 190.94
Western Pacific	Northwest Island, Australia	Shallow Island	Loggerhead, Green	324.00 $\pm$ 131.86
Western Pacific	Woongarra Coast, Australia	Coastal	Flatback, Loggerhead	371.37 $\pm$ 149.97
Western Pacific	Wreck Island, Australia	Shallow island	Loggerhead, Green	339.44 $\pm$ 129.94
Western Pacific	Wreck Rock Beach, Australia	Coastal	Loggerhead	324.23 $\pm$ 145.72
Western Pacific	Guam	Deep Island	Green	368.79 $\pm$ 122.68
Western Pacific	Alas Purwo, Indonesia	Coastal	Hawksbill, Olive Ridley	639.19 $\pm$ 346.51

Table 1. Cont.

Ocean Region	Site	Coast Type	Species	Mean Distance (km) $\pm$ SD
Western Pacific	Jamursba Medi, Indonesia	Shallow Island	Hawksbill, Green, Olive Ridley, Leatherback	604.16 $\pm$ 326.32
Western Pacific	Terengganu, Malaysia	Coastal	Hawksbill, Green, Olive Ridley, Leatherback	312.83 $\pm$ 121.41
Western Pacific	Khram Island, Thailand	Shallow Island	Hawksbill, Green	201.43 $\pm$ 73.22

2.3. Statistical Analysis

Transport Distance

We analyzed factors that could contribute to the variation in ocean transport distances for 67 sites worldwide, using the information-theoretic approach [32].

We included the year, ocean region, coast type, latitude, and longitude as factors in the model. The chosen factors represent large-scale spatiotemporal influences on transport [33]. Evaluating the yearly differences allowed us to examine inter-annual variability. The ocean regions are large basins with unique ocean currents and land mass obstructions, e.g., North Atlantic Ocean, Mediterranean Sea, Gulf of Mexico, etc. Coast type is a potential source of hatchling survival variability based on the bathymetry of the area surrounding the beach and the related predator density [34]. We defined coast type as either coastal, shallow island (within continental shelf), or deep island (off the continental shelf, usually mid-ocean). The geographic coordinates, i.e., latitude and longitude, allowed us to examine spatial trends on two gradients rather than by large units as in the ocean region factor. We analyzed both the transport distance and the standard deviation of transport distance as the response variables at our chosen temporal intervals (i.e., 1, 5, 10 and 30 days post-hatching).

Visual inspection of the residuals from a global linear model (which included all candidate explanatory variables) suggested deviation from a normal distribution and heteroscedasticity. Using variance inflation factors (VIF), we tested for collinearity of the explanatory variables. All variables had a VIF < 3, our a priori threshold, and all were included in the global model [35]. We checked the sites for spatial autocorrelation and found no evidence of spatial autocorrelation (based on Moran's I test). Initial exploratory analyses and ACF plots of transport distance regressed with the spatial factors and year indicated the presence of temporal autocorrelation with a 25+ year lag. Including an autocorrelation structure in the model substantially increased the model fit. However, we were specifically interested in modelling year as a fixed effect so that it would be acted upon during the model selection process, so we did not include year as a random effect. Thus, we used a generalized linear model and a gamma distribution with a log link.

2.4. Model Selection

We used the information-theoretic approach to evaluate which of the chosen factors influenced hatchling transport distance. We used Akaike Information Criterion correction for small sample sizes (AICc) to rank potential models [32,36]. Models included in the confidence set were those with a $\Delta\text{AICc} \leq 2$. These models were considered to balance parsimony in the number of explanatory variables while achieving a good fit to the data. We used relative importance (the sum of the AICc weight of the models in the confidence set containing a variable) to evaluate the importance of variables [32]. We used evidence ratios to compare the probability of the top-ranked models against the intercept-only null model [32].

3. Results

3.1. Global Patterns of Mean Transport Distance

In general, the relationships with modeled ocean driven hatchling transport and the explanatory variables were similar for each period examined (1, 5, 10, and 30 days), but were most pronounced at 30 days. Therefore, while we will be presenting figures including all transport periods, we primarily discuss transport at 30 days as the factors are most apparent at that interval (Figure 2). The range of the mean transport distance, using 30 days of hatchling transport from the nesting beaches, was 67 km (± 64.66 km standard deviation (SD)) in Chiriquí, Panama to 817 km (± 254.53 km SD) in the Galapagos Islands, Ecuador. Globally, the mean transport distance at 30 days across all sites was 307 km (± 151.74 km SD). Though the variation between sites was generally more pronounced, the inter-annual differences in transport for specific nesting beaches also appeared to vary depending on how the currents shift at that location for any given year. For example, in Australia, Gnaraloo Bay and Ningaloo have similar transport. Due to the similarity in transport at the two sites and the yearly variation of each site, in some years, Gnaraloo Bay has higher transport, such as 1996, but in 1998 Ningaloo had higher transport.

Figure 2. The hatchling transport distance for all sites after 30 days in relation to (A) Coast type, (B) Ocean region, (C) Latitude, and (D) Year. To improve visualization, ocean region has been square root transformed and the y-axis reduced so not all outliers are visible.

Latitude, coast type, and ocean region were always included in the model confidence set for each transport period and each had a relative importance of 1.0 (Table 2). Transport distance was greatest in the tropical latitudes. Overall, southern hemisphere sites had greater transport distance than northern hemisphere sites, although the sites farther north had less variability in transport over time. This pattern in latitude holds true for the whole short-term transport period we simulated though with differing magnitudes (Figures A1–A3, see Appendix A).

Table 2. Confidence set for models describing mean transport distance and standard deviation of transport distance from 1–30 days post-hatching. The + symbol indicates a categorical variable (coast type and ocean region) was included in a model set, whereas when continuous variables (latitude, longitude, and year) were included in a model set, the parameter estimate is reported, and the relative effect size is reported. Models are ranked by their AICc weight. The relative importance (RI) of each variable in the model for each transport period is listed below the selection.

Model	Coast Type	Ocean Region	Latitude	Longitude	Year	Degrees of Freedom	AICc	Δ AICc	AICc Weight
Mean 1 Day	+	+	−0.0065	0.00084	−0.0030	16	12,099.08	0	0.51819
	+	+	−0.0066		−0.0030	15	12,100.53	1.45644	0.25016
	+	+	−0.0066	0.00083		15	12,100.69	1.61037	0.23163
RI	1.0	1.0	1.0	0.75	0.77				
Mean 5 Days	+	+	−0.0061			14	16,479.79	0	0.32274
	+	+	−0.0060	0.00055		15	16,479.84	0.04512	0.31554
	+	+	−0.0061		−0.0013	15	16,480.93	1.13417	0.18305
	+	+	−0.0060	0.00055	−0.0013	16	16,480.98	1.18274	0.17866
RI	1.0	1.0	1.0	0.49	0.36				
Mean 10 Days	+	+	−0.0072			14	18,193.3	0	0.50573
	+	+	−0.0072	0.00033		15	18,194.53	1.23551	0.27266
	+	+	−0.0072		−0.0009	15	18,194.95	1.65027	0.2216
RI	1.0	1.0	1.0	0.27	0.22				
Mean 30 Days	+	+	−0.0073	0.0007		15	21,186.48	0	0.60369
	+	+	−0.0073			14	21,187.32	0.84177	0.39630
RI	1.0	1.0	1.0	0.6					
St Dev 1 Day		+	−0.0141	0.00067	−0.0071	14	9860.584	0	0.61589
		+	−0.0141		−0.0071	13	9861.528	0.94433	0.38410
RI		1.0	1.0	0.62	1.0				
St Dev 5 Days		+	−0.01631		−0.0045	13	14,570.51	0	0.63628
		+	−0.01627	−0.00037	−0.0045	14	14,571.63	1.11853	0.36371
RI		1.0	1.0	0.36	1.0				
St Dev 10 Days		+	−0.017			12	16,327.43	0	0.40193
		+	−0.01693	−0.00046		13	16,328.27	0.84260	0.26374
		+	−0.017		−0.0011	13	16,329.02	1.59193	0.18133
	+	+	−0.01685			14	16,329.36	1.93187	0.15298
	0.15	1.0	1.0	0.26	0.18				
St Dev 30 Days	+	+	−0.00974			14	18,977.83	0	0.71428
	+	+	−0.00973	−0.00023		15	18,979.66	1.83260	0.28571
RI	1.0	1.0	1.0	0.29					

The coast type and ocean region were consistently present in the model confidence set (Table 2). Coast type was a factor in all of the models across all transport periods. Modeled transport from coasts was generally lower than transport from deep or shallow islands (Figures 2 and 3). Deep islands had the highest transport distance, while shallow islands had slightly smaller average distances. Coastal sites never had the highest transport in any year. In contrast, there were only three years where shallow islands, rather than coasts, had the lowest transport distance.

Figure 3. Example sites illustrating the differences in coast type (A) and ocean region (B). The order and color of the sites correspond to the same metrics in Figure 2. Error bars have been omitted as they occlude patterns.

The ocean region of each site was also an important factor in all of the models in the confidence set across all transport periods. The Red Sea, Gulf of Mexico, Mediterranean Sea, and North Atlantic Ocean tended to have the lowest transport, while the Eastern Pacific and Indian Oceans tended to have the highest (Figures 2 and 4). Notably, despite the variability in transport distance at each site, the ocean regions had a relatively consistent mean transport distance relative to one another. The regions tended to have broad ranges with a large amount of overlap in values, but regions had consistent general ranges (Figure 2). Year and longitude appeared occasionally in the confidence set and had lower relative importance compared to latitude, coast type and ocean region.

3.2. Temporal Factors

There were distinct and extreme inter-annual fluctuations in the modeled transport distances of hatchling turtles. Shifts in ocean currents between years produced substantial fluctuations at individual sites (Figure 4). For example, the Galapagos Islands, Ecuador, changed from an average 30-day transport distance of 1103 km (± 216 km) in 1994 to 423 km (± 116 km) in 1995. Year did not, however, have a linear correlation with transport (Figure 2). Though inter-annual variation in currents impacted the transport from sites, there is no annual trend to suggest global changes in ocean currents effecting sea turtle transport within our study period.

3.3. Annual Variability in Hatchling Transport Distance

The patterns of variability of transport distances from each nesting beach had some notable patterns. First, variability in transport distance increased with the transport period (Figures 4, A4 and A5 see Appendix A). Second, coast types are not included in the confidence set until transport is measured for 10 days and is only present in all models in the confidence set after 30 days of transport (Table 2). Conversely to mean transport distance, year is present in all models of the confidence set at 1- and 5-days transport, and then nearly absent at 10- and 30-days (Table 2). Like mean transport distance, the ocean region and latitude were present in all models in the confidence set, with the Eastern Pacific having the highest standard deviation as well as the highest mean transport, while the Gulf of Mexico had the lowest standard deviation, and the Red Sea had the lowest mean transport distance (Figures 2 and 4).

4. Discussion

Sea turtle conservation is a global issue due to their broad distributions, highly migratory nature, and long history of exploitation of all species [37]. Therefore, comprehensive assessments of their life history and ecology at the global scale are an important and valuable tool [37,38]. Ocean circulation models have been used to evaluate transport of simulated particles away from specific regions or beaches, particularly for purposes of evaluating hatchling swimming [8,39–41] and predicting distributions of hatchlings [42–44]. Ocean circulation models have also been used for such diverse studies as finding the best places to release rehabilitated turtles and studying migratory ontogeny [25,45]. However, a global analysis of hatchling transport across all oceans and species has not been performed at this scale to date. The global patterns we have presented here provide evidence that the offshore transport of hatchling sea turtles is highly variable and may have profound impacts on the population dynamics of these species [2,42]. The combination of high spatial and temporal variability across nesting beaches globally indicates that sea turtles may rely on the portfolio effect to act as a buffer against the years and locations that are suboptimal and facilitates the survival of the population as a whole, even if certain beaches fail to produce many hatchlings during certain periods [46–49].

4.1. Spatial Factors

Our modelling approach indicates that ocean region, coast type, and latitude all play important roles in ocean driven sea turtle hatchling transport. There are clear differences in transport distance across ocean regions. Accounting for the regional differences in hatchling transport and the status of adult sea turtles could improve conservation assessments for specific populations. For example, populations exposed to nest poaching or adult bycatch that also have low transport potential could be especially vulnerable, as the estimated number of hatchlings recruiting to pelagic habitats may be lower than the mean for that population. Thus, information on transport potential combined with other ecological information may provide insight into what aspects of conservation may be confounded by transport based mortality. For instance, nesting beaches on mainlands (coastal coast type) tend to have lower transport distances than either deep or shallow islands (Figure 2A), which might result in higher predation as hatchlings attempt to migrate offshore to nursery habitat [15–17]. In such a setting, efforts to reduce terrestrial predators may not ultimately result in increased hatchling survival because of this coastal mortality bottleneck. However, such efforts to reduce terrestrial predators on oceanic islands might create a more noticeable increase in overall population growth as hatchlings are poised to quickly recruit to nursery habitat [34]. While there is high spatio-temporal variability in transport distance, there are relatively predictable rankings in transport across the ocean regions (Figures 2B and 4F), and which may provide insight into which populations might be more constrained by juvenile recruitment dynamics as compared to other stages of the sea turtle life cycle or by anthropogenic perturbations.

4.2. Temporal Factors

The year in which turtle hatchlings enter the sea from a nesting beach also influences transport distance, but not as frequently as the spatial factors. On a global scale, rather than a regional one, an annual trend is almost non-existent. Ocean currents are predicted to slow due to anthropogenic climate change [50]. However, in our 25-year analysis covering 67 nesting beaches, we do not see strong evidence of decreased hatchling transport from 1993 to 2017 (Figure 2). As offshore hatchling transport is an important factor contributing to neonate survival, this is encouraging information for these endangered and threatened species. Interestingly, several basins show inter-annual fluctuations that are likely consistent with large-scale fluctuations and climatic patterns within those regions. For example, the low transport fluctuation in the Eastern Pacific corresponds to the strong El Niño in 1997–1998, while the high transport fluctuation corresponds to the strong La Niña in 2007–2008 (Figure 2).

When sites are examined individually, there is considerable inter-annual variation in hatchling transport distances across the nesting beaches. Our research also indicates that no beach is characterized by consistently high or low current intensity. Thus, hatchling survival is also probably highly variable. As no site is “always” ideal, adult females are long-lived and nest over many years, and natal homing likely includes a broader area than traditionally assumed [51], it is likely that some diversity in nesting locations would be indefinitely maintained in the population. Even locations that tend to be unfavorable may have some years where hatchling cohorts are successfully transported to favorable habitat.

The high degree of inter-annual variation in hatchling transport underlines the importance of long-term studies to properly evaluate sea turtle conservation status. Basing hatchling survival estimates on a field study carried out in a single year may inadvertently skew the estimate based on the ocean currents at that time. In all, yearly differences matter just as much as regional ones when estimating population trends and evaluating management strategies. Furthermore, through the first month of transport, the influence of the spatial and temporal factors on hatchlings only intensifies from day one to thirty (Figure 2). An advantageous set of circumstances at hatching begets an expedited journey to the safety of the open ocean for the duration of early transport (Figure 3). Ultimately, this temporal variability may result in disproportionate contributions of sea turtle juvenile recruits from certain beaches within populations.

4.3. Model Uses, Future Directions, and Caveats

All sea turtles are threatened by anthropogenic activities [38,52,53]. Managing and protecting populations has become vital in the effort to increase populations, and in some populations, recovery is evident [37]. Population models help researchers and managers estimate the population size, recovery time, and how to best protect the species [54–56]. To correctly model populations, accurately estimated life history traits are necessary, including hatchling survival [56–58]. Presently, many population models use a static value determined by mark-recapture studies, internal model fitting, life tables, or data sharing from other more studied species for good reason [54,59–61]. Currently, it is logistically challenging, if not prohibitive, to estimate the survival of an entire hatchling cohort or track them via satellite before they reach a size almost twice the length of newly born turtles [62,63]. However, understanding how the environment plays a role in determining when a hatchling reaches the relative safety of the open ocean could help parameterize population models with a more accurate value relative to the “normal” performance of the beach or the region. Understanding that not all natal beaches are equal, in terms of transport, and ultimately hatchling survival, may help scientists to tailor models and management more specifically to better direct efforts to the maximum effect for these turtles. However, there are additional factors to be considered, such as region-specific threats to turtles, and specific conservation actions that were beyond the geographical scope of this paper. Furthermore, a nesting beach with ideal physical conditions could still have a negative growth rate, if the turtles in the area have increased mortality that outweighs the

benefits of the hatching beach as anthropogenic threats can impact populations to extreme degrees [38,64].

Future steps in understanding the factors affecting hatchling transport would relate the short-term survival of hatchlings from several of the sites to the speed of local ocean currents and predicted transport distance. Acoustic tagging for longer periods would be useful to estimate survival for neonate turtles, though, perhaps, logistically complicated to implement [14,65,66]. Acoustic tagging has recently been used to estimate hatchling mortality as well, a more technologically advanced, and possibly more accurate, method than that used in the past [17]. As our model did not include swimming turtles, only the environmentally based movement, tagging and tracking would help improve the model estimates of movement along with mortality. Additionally, relating the population abundance or growth to the transport distance could validate the connection between high transport distance and higher hatchling survival and recruitment into the adult population. However, this relationship could be confounded by sources of mortality for later age classes, such as bycatch. The survival of large juveniles and sub-adults has a greater impact on population growth rate, as these age classes are poised to contribute to reproduction, yet survival is still lower than adults [54]. However, these studies did not consider the range or magnitude of hatchling survival, temporal variability, or density-dependence in neonate production. Using a modeling approach to estimate hatchling transport is a cost effective and simple tool that, particularly if paired with field studies in the future, can improve demographic models and conservation planning.

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Appendix A

Table A1. Nesting beach sites included in the study, organized alphabetically by Ocean Region and then by country as in Table 1. Each site is listed with the coordinates of the center of the release zone.

Site	Latitude (Decimal Degrees)	Longitude (Decimal Degrees)
Long Island, Antigua	17.1542	−61.7542
Tortola, British Virgin Islands	18.6208	−65.6167
Klein Bonaire Beaches, Caribbean Netherlands	12.15	−68.3014

Table A1. *Cont.*

Site	Latitude (Decimal Degrees)	Longitude (Decimal Degrees)
Cahuita National Park, Costa Rica	10.15	−82.8875
Grandoca, Costa Rica	10.4236	−82.5903
Tortuguero, Costa Rica	10.5403	−83.4903
Culebra Island, Puerto Rico	18.4667	−65.45
Fajardo-Luquillo, Puerto Rico	18.8681	−65.6903
St. Croix National Wildlife Refuge, US Virgin Islands	17.0667	−65.3042
Ostional, Costa Rica	9.0667	−86.1681
Galapagos Islands, Ecuador	−0.6	−90.7
Chiriqui, Panama	8.1875	−82.3042
Dry Tortugas-Loggerhead Key, US Florida	24.6181	−82.9208
Gulf Islands National Sea Shore, US Florida	30.3514	−86.0667
Siesta Key, US Florida	27.25	−83.0014
Campeche, Mexico	20.0847	−90.7875
Rancho Nuevo, Mexico	23.6167	−98.2667
Veracruz, Mexico	20.8	−97.0167
Padre Island, US Texas	27.3847	−97.5833
Cable Beach, Australia	−17.7403	122.0167
Gnaraloo Bay, Australia	−23.8	114.0347
Ningaloo, Australia	−22.6736	114.1542
Peak Island, Australia	−21.6014	114.4903
Europa Island, French Southern Territories	−22.3667	40.2875
Glorieuses Island, French Southern Territories	−11.5042	47.2069
Tromelin Island, French Southern Territories	−15.8681	54.5208
Gahirmatha, India	20.7375	87.0069
Mayotte, Mayotte	−13.1875	45.1542
Ponta do Ouro, Mozambique	−26.8542	32.1333
Karachi, Pakistan	24.9736	67.6569
Silhouette Island, Seychelles	−4.4903	55.2236
Kyparissa Town, Greece	37.0833	21.4167
Zakynthos, Greece	37.4172	21.5833
El Mansouri, Lebanon	33.1736	35.15
Kurait, Tunisia	36.0181	11.1333
Dalyan Beach, Turkey	36.0347	28.8681
Fethiye Beach, Turkey	36.0833	29.2403
Goksu Delta, Turkey	36.2569	34.5375
Patara Beach, Turkey	36.5347	29.2708
Archie Carr National Wildlife Refuge, US Florida	28.3375	−80.5014
Amelia Island, US Florida	30.6	−81.4014

Table A1. *Cont.*

Site	Latitude (Decimal Degrees)	Longitude (Decimal Degrees)
Canaveral Air Force Station, US Florida	28.4833	−80.5181
Wassaw, US Georgia	31.85	−80.9181
Bald Head Island, US North Carolina	33.8542	−78.1347
Huntington Beach State Park, US South Carolina	33.0667	−79.0375
Hunting Island SP, US South Carolina	32.35	−80.4736
French Frigate Shoals, US Hawaii	23.1333	−166.45
Miyazaki, Japan	31.3514	131.5708
Jazā'ir Jiftūn, Egypt	27.2208	34.1208
Wadi el Gemal, Egypt	24.05	35.5569
Zabargad, Egypt	23.6	36.1833
Ascension Island	−8.4333	−14.5014
Bahia, Brazil	−12.5736	−38.3181
Espirito Santo, Brazil	−18.4167	−39.85
Congo Coast, Congo	−4.9736	11.2236
Bioko Island, Guinea	3.4	9.0236
Heron Island, Australia	−23.4347	151.9014
Milman Island, Australia	−11.1181	143.0014
Northwest Island, Australia	−23.2847	151.7
Woongarra Coast, Australia	−24.7847	152.4347
Wreck Island, Australia	−23.3181	152.2847
Wreck Rock Beach, Australia	−23.0167	152.0833
Guam	13.4736	144.9833
Alas Purwo, Indonesia	−9.3042	114.2069
Jamursba Medi, Indonesia	−0.2	132.6208
Terengganu, Malaysia	5.3681	103.4681
Khram Island, Thailand	12.3514	100.7875

Figure A1. The hatchling dispersal distance for all sites after 1 day represented in relation to (A) Coast type, (B) Ocean region, (C) Year, and (D) Latitude. Ocean region has been square root transformed and the graph range reduced so not all outliers are visible.

Figure A2. The hatchling dispersal distance for all sites after 5 days represented in relation to (A) Coast type, (B) Ocean region, (C) Year, and (D) Latitude. Ocean region has been square root transformed and the graph range reduced so not all outliers are visible.

Figure A3. The hatchling dispersal distance for all sites after 10 days represented in relation to (A) Coast type, (B) Ocean region, (C) Year, and (D) Latitude. Ocean region has been square root transformed and the graph range reduced so not all outliers are visible.

Figure A4. The standard deviation of Transport distance for all sites after 5 days in relation to (A) Coast type, (B) Ocean region, (C) Year, and (D) Latitude. The y-axis for (B) Ocean region has been square root transformed and reduced so not all outliers are visible. Error bars have been omitted as they occlude patterns.

Figure A5. The standard deviation of Transport distance for all sites after 10 days in relation to (A) Coast type, (B) Ocean region, (C) Year, and (D) Latitude. The y-axis for (B) Ocean region has been square root transformed and reduced so not all outliers are visible. Error bars have been omitted as they occlude patterns.

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