

Spatio-temporal variation in ocean current-driven hatchling dispersion: Implications for the world's largest leatherback sea turtle nesting region

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Abstract

Aim: The lives of juvenile leatherback turtles are amongst the most enigmatic of all marine mega-vertebrates. For these cryptic organisms, ocean models provide important insights into their dispersion from natal sites. Here, corroborated by fisheries by-catch data, we simulate spatio-temporal variation in hatchling dispersion patterns over five decades from the World's largest leatherback turtle nesting region.

Location: Equatorial Central West Africa (3.5°N to -6°S) spanning the Gulf of Guinea in the North, Gabon and the Republic/Democratic Republic of the Congo in the South.

Results: Due to dynamic oceanic conditions at these equatorial latitudes, dispersion scenarios differed significantly: (1) along the north to south gradient of the study region, (2) seasonally and (3) between years. From rookeries to the north of the equator, simulated hatchling retention rates within the Gulf of Guinea were very high (>99%) after 6 months of drift, whilst south of the equator, retention rates were as low as c. 6% with the majority of simulated hatchlings dispersing west into the South Atlantic Ocean with the South Equatorial Current. Seasonal dispersion variability was driven by wind changes arising from the yearly north/southward migration of the intertropical convergence zone resulting in the increasing westerly dispersion of hatchlings throughout the hatching season. Annual variability in wind stress drove a long-term trend for decreased retention within the Gulf of Guinea and increased westerly dispersion into habitats in the South Atlantic Ocean.

Main conclusions: Shifts in dispersion habitats arising from spatio-temporal oceanic variability expose hatchlings to different environments and threats that will influence important life history attributes such as juvenile growth/survival rates; anticipated to impact the population dynamics and size/age structure of populations into adulthood. The impacts of local and dynamic oceanic conditions thus require careful considerations, such as subregional management, when managing marine populations of conservation concern.

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KEYWORDS

animal migration, animal movement, *Dermochelys coriacea*, dynamic ocean conditions, Gabon, general ocean circulation models, hatchling dispersal, Lagrangian analyses Leatherback sea turtle, marine dispersal

1 | INTRODUCTION

Dispersal with ocean currents is a pervasive life history strategy driving major ecological processes such as population dynamics, connectivity and ensuring the progeny of a range of marine taxa reach suitable settlement or development sites (Ascani, Van Houtan, Di Lorenzo, Polovina, & Jones, 2016; Baltazar-Soares et al., 2014; Kendall, Poti, & Karnauskas, 2016; Planes, Jones, & Thorrold, 2014). Aided by ocean currents, the dispersal distances of small marine organisms like juvenile sea turtles (Boyle et al., 2009) can rival the migration distances of the most powerful marine mega-vertebrates such as the great whales (Mate et al., 2015). However, as conventional animal tracking devices are too large to track small organisms, their movements remain enigmatic (Hazen et al., 2012). Indeed, the period when neonate hatchling sea turtles disperse from their natal beaches to oceanic development habitats is known as the “lost years” (after Carr, 1986) as hatchlings emerge from nests and then disappear into the sea. For some sea turtle populations, key juvenile development habitats have been identified from fisheries bycatch data. For juvenile turtles caught by fishers in waters around Peru, the Azores and Baja California, their DNA enabled their natal rookery of origin to be traced back to Australia, the USA and Japan, respectively, with ocean currents identified as the key determinant linking natal nesting sites and distribution patterns (Bolten et al., 1998; Bowen et al., 1995; Boyle et al., 2009; Monzón-Argüello et al., 2010; Naro-Maciel et al., 2014). Nevertheless, for most sea turtle populations, the whereabouts of juvenile life stages are unknown. Ocean models have thus become a valuable tool for studying the cryptic lost years and by combining ocean modelling and biological approaches novel assessments can be made into the anthropogenic threats juvenile turtles face, their behavioural ontogeny and important life history attributes such as juvenile growth rates and population dynamics into adulthood (e.g., Ascani et al., 2016; Casale & Mariani, 2014; Hays, Fossette, Katselidis, Mariani, & Schofield, 2010; Putman, Scott, Verley, Marsh, & Hays, 2012; Putman, Verley, & Lohmann, 2012; Putman et al., 2015; Scott, Marsh, & Hays, 2012a; Scott, Marsh, & Hays, 2014).

The leatherback sea turtle (*Dermochelys coriacea*) is the largest most vagile sea turtle species and the movements of satellite-tracked adult turtles routinely span entire ocean basins (e.g., Benson et al., 2011; Fossette et al., 2014). However, very little is known about juvenile life stages and records of their at-sea locations are sparse. For example, a global review of juvenile leatherback turtles encountered as bycatch contained data on just 10 individuals <60 cm straight carapace length (SCL) (Eckert, 2002), whilst thousands of small juvenile loggerhead turtles (<60 cm SCL) have been encountered in the North East Atlantic fisheries alone (Bjørndal, Bolten, & Martins, 2003). The

infamous “lost years” of juvenile leatherback turtles thus remains one of the biggest mysteries surrounding sea turtle life histories. Knowledge of their behaviours is also sparse due to difficulties associated with rearing and observing this species in captivity (Jones, Salmon, Wyneken, & Johnson, 2000). Nevertheless, leatherback turtles are considered obligate gelatinivores; preying on gelatinous zooplankton; for example, jellyfish and ctenophores (Bjørndal, 1997; Dodge, Logan, & Luttcavage, 2011) and juveniles are thought to require their body mass in prey every day to sustain growth rates (Luttcavage & Lutz, 1986). Consequently, ocean currents are a key determinant of their distribution because juvenile turtles require productive foraging habitats such as nutrient-rich upwellings and ocean currents play a crucial role in driving the formation of upwellings (Behrenfeld et al., 2006) and shaping the distributions of small marine organisms like neonate turtles and their prey (Monzón-Argüello et al., 2010; Moon, Pang, Yang, & Yoon, 2010). Furthermore, the importance of oceanic processes for adult leatherback turtles is already well documented; satellite-tracked turtles are known to migrate to nutrient-rich waters (e.g., Block et al., 2011; Witt et al., 2011), their foraging movements can be strongly influenced by the movement trajectories of ocean current flows (Lambardi, Lutjeharms, Mencacci, Hays, & Luschi, 2008), and long-term oceanic cycles influence characteristics of breeding populations (Robinson et al., 2014).

With the wealth of satellite tracking datasets now available (Jeffers & Godley, 2016), efforts aimed at affording better protection to turtles away from their breeding grounds (where conservation efforts have focussed: Hamann et al., 2010) are gaining momentum (e.g., Fukioka and Halpin, 2014; Hart, Lamont, Fujisaki, Tucker, & Carthy, 2012; Shillinger et al., 2008). In particular, the recent move towards dynamic ocean management approaches, in which the timing and location of conservation legislation changes at spatio-temporal scales that reflect changing marine environments and turtle distributions show considerable promise (Howell, Kobayashi, Parker, & Balazs, 2008; Maxwell, Ban, & Morgan, 2014; Maxwell et al., 2015). However, we need a much greater understanding into the habitats, behaviours and implications of dynamic oceanic conditions for juvenile life stages to more fully protect sea turtle populations from hatchlings into adulthood. Despite dramatic declines (>97%) for some leatherback turtle populations in the Pacific over the past few decades (see Wallace, Tiwari, & Girondot, 2013), the South Atlantic has remained a major stronghold with Gabon (Central West Africa) hosting the world's largest leatherback turtle nesting rookery (>40,000 nests/year; Witt et al., 2009). Bordering Gabon to the north and south of the equator (from 3.5°N to 6°S), Equatorial Guinea (specifically Bioko Island) and the Democratic Republic and the Republic of the Congo also host around 300 and 3,000 nests per year (see Wallace et al., 2013). Here, we use

a state-of-the-art ocean circulation model to study spatio-temporal variation in local oceanic conditions across this large equatorial region (over a period of five decades) to assess the implications for dispersing leatherback hatchlings and globally important Central West African populations into adulthood.

2 | METHODS

2.1 | Ocean model

Ocean circulation patterns were investigated with the high-resolution ocean general circulation model TRATL01 (Duteil, Schwarzkopf, Böning, & Oschlies, 2014). This model configuration is based on the Nucleus for European Modelling of the Ocean code (NEMO: Madec, 2008) developed in the European Drakkar cooperation (Barnier et al., 2007). A horizontally refined grid (AGRIF: Debreu, Vouland, & Blayo, 2008), representing the mesoscale with a resolution of $1/10^\circ$ in the tropical Atlantic (c. 15 km between 30°S – 30°N), is nested within the global $1/2^\circ$ model grid ORCA05. A 60-year hind-cast experiment was simulated using CORE atmospheric forcing of the years 1948–2007 (Large & Yeager, 2009). The atmospheric forcing is applied at six-hourly resolution and thus includes short-term events like tropical storms. Using simulated velocity output updated at a 5-day temporal resolution, virtual floats (representing virtual hatchlings) were advected with the model's surface ocean flow fields using Ariane particle trajectory software (Blanke, Speich, Madec, & Doos, 2001). Floats were constrained within Ariane to remain within depths of 0–6 m due to the positive buoyancy of hatchlings. Floats were first assigned to one of 20,000 random release locations within a large release area 125–400 km offshore from nesting beaches throughout the Republic/Democratic Republic of the Congo (from hereafter referred to as “the Congo region”), Gabon and Equatorial Guinea spanning latitudes of c. 6°S to 3.5°N . This offshore release zone brackets a range of locations hatchling leatherback turtles might reach assuming a sustained offshore swimming frenzy (Wyneken & Salmon, 1992) whilst under the influence of variable near-coastal processes (e.g., tides) and accounting for the fact that the model was not specifically set up to represent nearshore processes. For each month over the 4-month long hatching season (January–April), each of the 20,000 floats was assigned a random release day and drift simulations ran every year during the period 1960–2007 resulting in drift trajectories of approx. 4 million virtual floats. To identify the initial dispersion areas of post-hatchlings and small juvenile turtles, our analyses focused on the first 6 months of drift.

2.2 | Spatial variability

Data were analysed using a combination of Ferret, R and ArcGIS software and by constructing probability maps of float locations (e.g., Gary, Lozier, Böning, & Biastoch, 2011). To investigate spatial variability in ocean currents across the different nesting sites in this region, floats were isolated from six latitudinal bands (Figure 1): (a) Equatorial Guinea (specifically, Bioko Island in the Gulf of Guinea (c. 3.5 – 1°N), (b) north Gabon (specifically Pongara National Park; c. 1.0°N to 0.1°S

degrees), (c) central Gabon (c. 0.1° to 3.3°S), (d) south Gabon (specifically Mayumba National Park; c. 3.3° – 4.5°S) and (e) the Congo region (c. 4.5 – 6°S). Gabon was split into three regions (north, central and south) as nesting density data for Gabon revealed nesting densities vary considerably along Gabon's c. 900 km of coastline with the majority of nests concentrated in Pongara National Park in the North (c. 27% of nests along c. 26 km of beach) and Mayumba National Park in the South (c. 47% of nests along c. 60 km) (Witt et al., 2009). For each nesting region, core dispersion areas (defined based on 50% kernel utilization distributions) and dispersion ranges (defined as 90% kernel utilization distributions) were calculated. When calculating kernels, land barriers were taken into account following established methodologies (MacLeod, 2013). These areas were calculated to provide the clearest visual representation of any spatial overlap in predicted dispersion areas from different rookeries and between adult and juvenile sea turtles. R software was used to calculate mean dispersion bearings and displacement distances between starting locations and each time step using the geosphere and circular packages. Within Gabon, weighted dispersion statistics were also calculated based on nesting density data with floats released from North and South Gabon given a relative higher weighting (27% and 47%, respectively) than floats from central Gabon (Witt et al., 2009). We also included nine new and 28 previously published (Witt et al., 2011) satellite tracking data of adult sea turtles tracked between 2005 and 2013 from nesting beaches in the North and South of Gabon to assess any spatial overlap between core use areas of adult and juvenile turtles.

2.3 | Temporal variability

To investigate seasonal variability of the large-scale circulation, in particular the dynamics of the South Equatorial Current (SEC), we used zonal transport (latitudinal east to west transport) of water masses in the upper layer of the model (averaged from 10°W to 5°E and summed up from 15°S to 7°N to cover all branches of the SEC) as a proxy for westward dispersal correlated against model mean monthly wind stress values. To investigate interannual variability, we focused on oceanic conditions across the breadth of Gabon's coastline as this region captured the full range of potential hatchling dispersal scenarios (retention within the Gulf of Guinea and westward propagation within both the central [cSEC] and northern branches [nSEC] of the SEC). Temporal variability in dispersion patterns was investigated using the following metrics: (1) annual float numbers that reached 10°W after 6 months of drift as a proxy for westward dispersal and (2) annual float numbers that remained north of 1.5°S and east of 10°W as a proxy for retention rates within the Gulf of Guinea. Variability of these dispersion metrics was analysed by calculating a 11-year moving average to smooth out short-term fluctuations and investigate long-term trends/cycles over the 48-year time period 1960–2007 (low-pass filter). This smoothed time series was then subtracted from our initial dataset to investigate short-term interannual variability (high-pass filter). Oceanic time series datasets contain variability on various time-scales driven by different processes; hence, this technique enabled us to assess processes driving short- and long-term variability separately.

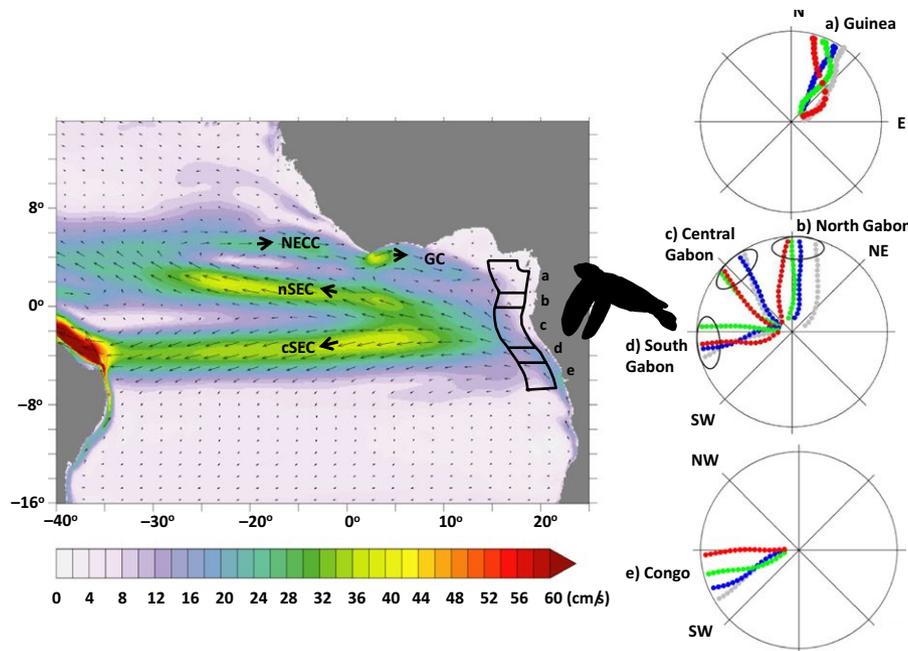


FIGURE 1 Regional oceanic conditions. Left panel: Mean surface current flows (climatological average from January to July) across our study region covering the four-month long hatchling season and a hatchlings subsequent first ≥ 3 months at sea. Current vectors are plotted along with speed of the surface currents (shading) averaged over the years 1960 to 2007. The major current flows impacting our nesting sites are also highlighted in bold: the easterly flowing Guinea Current (GC) and North Equatorial Counter current (NECC) and the westerly flowing northern (nSEC) and central (cSEC) branches of the South Equatorial current (SEC). Release zones (a-e) of virtual hatchlings from each nesting region are also outlined in black. Regions correspond to a) Equatorial Guinea (Bioko Island), b) North Gabon (Pongara National Park), c) Central Gabon, d) South Gabon (Mayumba National Park) and e) The Congo/Democratic Republic of the Congo. Right panel: Mean drift bearings of hatchlings are plotted every 5 days from drift day 5 (central bearing) to \sim drift day 90 (perimeter bearing) to highlight prevailing offshore current flows hatchlings would encounter from each nesting region (in the middle panel the three regions within Gabon are delineated by ellipses). Bearing data are plotted separately for each month (grey=Jan, blue=Feb, green=March, red=April) highlighting low seasonal variability (see also supplementary table 1 for mean and SD drift bearings after 1,3 and 6 months of drift).

To assess wind as a possible driver of large-scale upper ocean variability, we employed the same technique to study long- and short-term trends for annual mean wind stress magnitude data (averaged along 10°W from 15°S to the coast of Liberia). The Southern Hemisphere trade winds cross the equator and reach the Gulf of Guinea, resulting in a northerly component of wind stress throughout the eastern part of our study domain. Due to the Earth's rotation, which drives the Coriolis force, the effect of local wind patterns on hatchling dispersion will differ to the north and south of the equator. Surface currents will be deflected (by the process of Ekman drift) to the left of the direction of the wind stress (supporting westward dispersal) in the Southern Hemisphere and to the right of the direction of wind stress (suppressing westward dispersal) in the Northern Hemisphere. The effect of the wind stress is therefore analysed separately for the northern and the Southern Hemisphere.

3 | RESULTS

3.1 | Local oceanic conditions

Oceanic conditions are strongly dominated by the equatorial current system in the tropical Atlantic which varied on mesoscale and

decadal timescales. Whilst the general structure of the alternating zonal jets on and around the equator is well described (e.g., Brandt et al., 2011), open questions remain on the detailed current structure in the eastern tropical Atlantic. This is particularly apparent when comparing surface velocities (Figure 1, left panel) with large-scale geostrophic currents more representative of the general upper ocean (Figure S1). Initially, coastal currents in our model (Stramma & Schott, 1999; Strub, Combes, Shillington, & Pizarro, 2013) would transport hatchlings either north and into the Gulf of Guinea or south towards Angola. Within the Gulf of Guinea, the eastward North Equatorial Counter Current (NECC) feeds into the Guinea Current which flows east along the coast of Guinea suppressing westward propagation of floats. Oceanic conditions within the gulf resulted in high retention rates of virtual hatchlings and those that were not retained in the gulf were instead advected offshore and into the South Atlantic Ocean with the westward flowing branches of the SEC, specifically, the northern (nSEC), and more southerly central (cSEC) branches. The nSEC transported drifters offshore from the Gulf of Guinea towards the very north of Brazil/French Guinea, whilst the cSEC transported hatchlings offshore from Angola and towards north-western Brazil. Within 6 months of drift, drifters in the SEC could reach cross the South Atlantic Ocean reaching the coast of Brazil.

3.2 | Spatial variability

Spatial variability of hatchling drift scenarios was high along the north–south gradient of our study area due to the greater influence of the westward flowing cSEC and nSEC at southerly and more central latitudes (from central/south Gabon to the Congo region) and the northerly (Congo) and easterly (Guinea) flowing coastal currents at more northerly latitudes (from central/northern Gabon to Equatorial Guinea; Figure 1). As hatchling dispersed from their initial natal areas, these local current flows resulted in the mean initial drift trajectories (across the full time series) ranging from predominantly westerly/south-westerly routes into the South Atlantic Ocean from the most southern nesting extent (the Congo region; Figure 1 right bottom panel; Table S1) to predominantly northerly/north-easterly routes into the Gulf of Guinea from the most northern nesting extent (Bioko Island; Figure 1 right upper panel; Table S1). Within Gabon, hatchlings were advected along predominantly westerly routes into the Atlantic from the south, predominantly north-westerly routes from central Gabon and predominantly northerly routes from the north. As a result of these initial local oceanic conditions, three main dispersion regions emerged. From Bioko Island, north and central Gabon core dispersion areas were confined to within the Gulf of Guinea (Figure 2a–c). From south Gabon, two core areas emerged encompassing a relatively large region of the Gulf of Guinea and a second large region located within the central branch of the SEC extending across the South Atlantic towards the west coast of Brazil (Figure 2d). From the Congo region, a large core area also extended across the central branch of the SEC across the South Atlantic towards Brazil, whilst within the Gulf of Guinea, there was a relatively small core area (Figure 2e). Due to these different dispersion regions, displacement distances after 6 months of drift were highly variable with distances from nesting sites south of the Equator (central/south Gabon and the Congo region) of up to $3,229 \pm 1,715$ km (mean \pm SD) compared to sites north of the Equator (North Gabon and Bioko Island) of up to 450 ± 321 km (Table S1). Furthermore, retention rates of drifters within the Gulf of Guinea (defined here as north of 1.5° S and east of 10° W) differed across our nesting sites with retention rates of drifters in the Gulf of Guinea of >99% from Bioko Island and Northern Gabon, 65% and 39% from Central and Southern Gabon and <6% from the Congo region.

3.3 | Seasonal variability

Within each of the five nesting regions, mean dispersion directions were similar across the 4-month hatchling season (Figure 1, right panel); however, seasonal variation in mean displacement distances was highly variable for the three most southerly nesting sites (Table S1; Figure S2). For example, within 6 months of drift, the mean displacement distances (mean \pm SD km) of drifters released in April were over double those released in January from the Congo region (January: $1,298 \pm 816$, April: $2,656 \pm 1,446$), South Gabon (January: $1,581 \pm 981$, April: $3,229 \pm 1,715$) and Central Gabon (January: $1,298 \pm 816$, April: $2,656 \pm 1,446$). From North Gabon and Bioko

Island, travel distances were similar throughout the hatchling season (range: 432–450 and 314–330 between January–April, respectively). Unlike displacement distances, there were no trends in retention rates within the Gulf of Guinea which remained stable throughout the season; monthly retention rates of drifters (% of floats annually that remained north of 1.5° S and east of 10° W) were consistently >99% from Equatorial Guinea and north Gabon and ranged between 61% and 68% from central Gabon, 14%–19% from south Gabon and 3%–6% from the Congo region. Seasonality in westward displacement in the Southern Hemisphere could be explained by changes in mean monthly wind stress magnitude driven by the position of the Intertropical Convergence Zone (ITCZ) as it migrates north/southwards throughout the year (Figure S3). As the ITCZ migrates north (from January to July/August), the wind stress pattern also shifts north resulting in an increase in wind stress magnitude in the Southern Hemisphere and subsequent increase in westward transport throughout the hatchling season (Figure S4; 0-day lagged correlation: -0.82 , p -value: $<.005$). In the Northern Hemisphere, wind stress strength does not change throughout the hatchling season resulting in an almost constant transport in the upper layer of the Guinea current and thus lack of seasonality in hatchling retention rates in the Gulf of Guinea. In both hemispheres, wind direction remains fairly constant resulting in no clear seasonality in hatching dispersal directions (Figure 1; right panel).

3.4 | Interannual to decadal variability

The dispersion of floats showed prominent variability on timescales ≥ 1 year. For example, within 6 months of drift, 5% of floats propagated west of 10° W in 1971 compared to 56% of floats in 1994 and 83% of floats were retained in the Gulf of Guinea in 1972 compared to 33% in 2002 (Figure 4 top panel). Across the five decade time series, wind stress magnitude increased in the Southern Hemisphere but decreased in the Northern Hemisphere (Figure 4 bottom panel). These wind stress patterns seemed to drive an overall trend (as part of a decadal variability in ocean currents) for an increase in the rates of floats that dispersed west and a decrease in the retention rates of floats in the Gulf of Guinea (correlation between westward dispersal and (1) wind stress in the Northern Hemisphere: -0.93 (2) Southern Hemisphere: 0.64 and (3) retention rates: -0.67 , $p < 1\%$ in all cases). These long-term changes occurred due to a weakening of the Guinea Current and the strengthening of the westward cSEC/nSEC (Figure S5); consequently, floats that were previously retained within the Gulf of Guinea were advected westward (Figure 3). Nevertheless, these trends can arise from decadal variability which cannot be fully resolved across just five decades of data. In contrast to the decadal variability, interannual variability of westward dispersal on shorter timescales showed no significant correlation with variability of wind stress or retention rates and seemed to be driven by internal oceanic variability (Figure S6). Instead, because westward dispersal and retention rates were not anticorrelated, an increase/decrease in westward spread resulted from a stronger/weaker westward advection of floats that were not retained in the Gulf of Guinea.

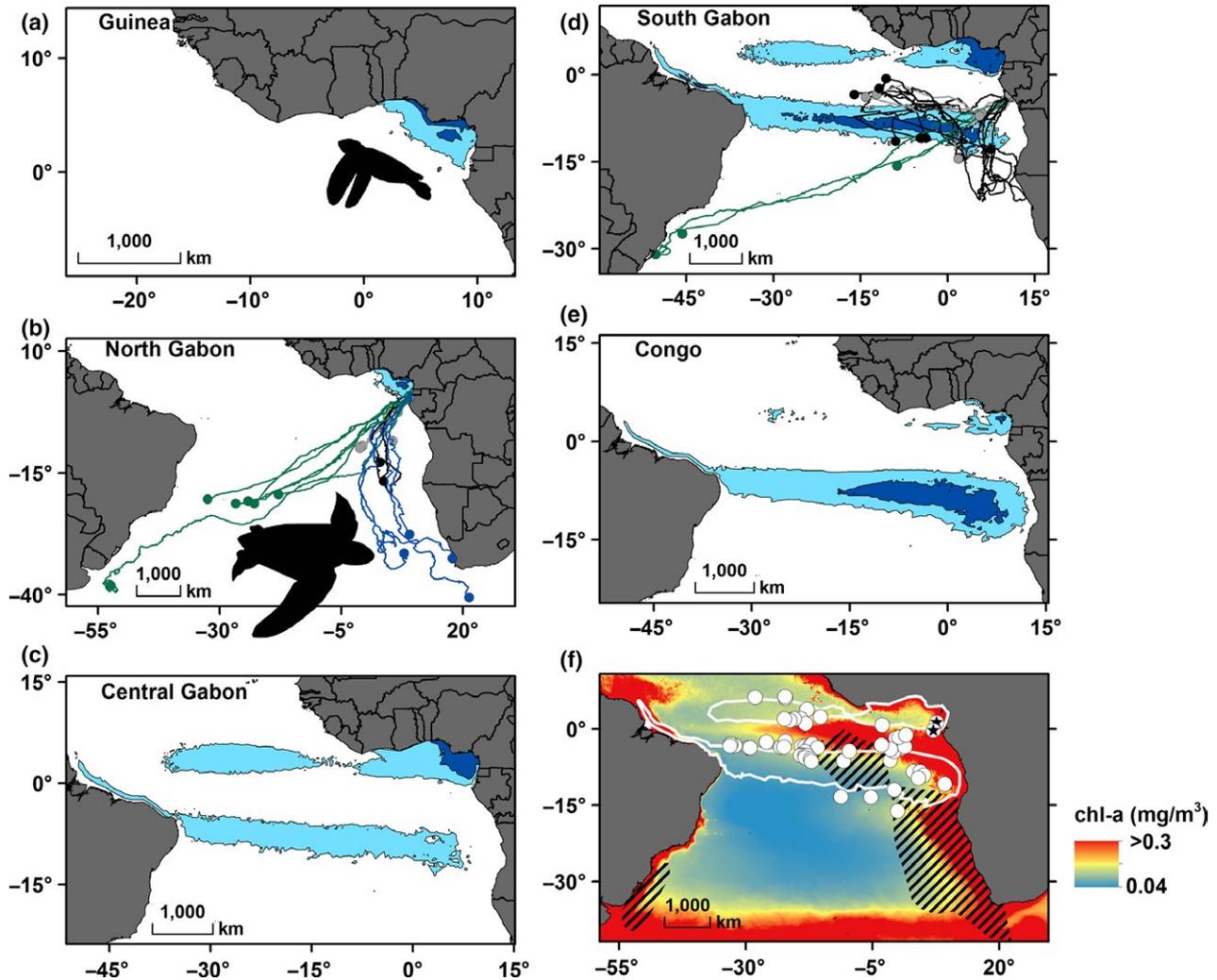


FIGURE 2 Core hatchling dispersion areas and ranges. For each nesting region (a–e) core hatchling development areas corresponding to the 50% kernel utilization distributions (dark blue) are plotted along with dispersion ranges corresponding to the 90% kernel utilization distributions (light blue). For Northern (b) and Southern (d) Gabon the migrations of adult leatherback turtles satellite tracked from these two regions are also plotted (unpublished data and data from Witt et al., 2011). For adult turtles, black lines and circles correspond to migration routes and final locations (respectively) for turtles that travelled to foraging regions in the central South Atlantic, whilst turtles depicted in green and blue migrated to feeding areas in South America and South Africa (respectively). For turtles depicted in grey their foraging strategy could not be determined due to premature cessation of ARGOS tag transmissions. (f) The full extent of our predicted hatchling dispersion regions (across all nesting regions) are also plotted (white outline) along with observational data of the locations of small juvenile turtles (c. 17 cm SCL) encountered in the Gulf of Guinea (white circles with black stars; digitized from Eckert, 2002) and larger juvenile turtles (60–100 cm SCL) encountered throughout the South Atlantic (white circles; digitized from Huang, 2015). Data in figure f are also overlaid onto mean chlorophyll a data (averaged over 2002–2015 from the Aqua MODIS sensor) and the general foraging regions of adult sea turtles tracked from Gabon are also highlighted (black dashed areas)

4 | DISCUSSION

By simulating the dispersion of hatchling leatherback sea turtles over a period of c. 5 decades, we predict key juvenile development habitats and discuss important implications of spatio-temporal oceanic variability for hatchlings from within the world's largest leatherback turtle nesting region. Across the north–south gradient of our study region, modelled hatchling dispersal scenarios differed significantly; virtual hatchlings north of the equator were exposed to predominantly northerly–north-easterly currents flowing into the Gulf

of Guinea, whilst those south of the equator were exposed to predominantly westerly–south-westerly currents flowing into the South Atlantic Ocean (Figure 1). From Equatorial Guinea, north, central and south Gabon, local oceanic conditions resulted in high retention rates in the Gulf of Guinea (up to 99.8%) with the easterly flowing North Equatorial Current and Guinea Current suppressing any passive westward dispersion (Figure 2a–c). Interestingly, there are only three reports of small juvenile leatherback turtles (<60 cm SCL) encountered in the South Atlantic and these were all located in the Gulf of Guinea (Eckert, 2002). Based on juvenile leatherback turtle growth

rate equations (Jones, Hastings, Bostrom, Pauly, & Jones, 2011), these three turtles (c. 17 cm SCL) are estimated to be c. 4 months of age and anecdotally support our predictions that the Gulf of Guinea is an important development habitat. Indeed, the Gulf of Guinea is one of the world's most productive marine areas due to year round nutrient-rich upwelling (Roy, 1995) and should thus provide excellent foraging opportunities for juvenile turtles. From the Congo region, very few drifters entered the Gulf of Guinea (with rates as low as 5% of drifters). Instead, the westerly cSEC and nSEC currents transported hatchlings into one of two large zones that spanned offshore from Angola (south of the equator) or Liberia (north of the equator) and across the South Atlantic Ocean towards the north-west coast of Brazil (Figure 2d–e). Reassuringly, recent reports of the distributions of large juvenile turtles (60–100 cm SCL) from fisheries bycatch data in the South Atlantic (Huang, 2015) correlated well with our dispersal predictions; observed and predicted distributions spanned the breadth of the South Atlantic confined to latitudes north of around 15°S (Figure 2f).

The high degree of spatial variability in dispersion scenarios we observed supports previous studies based on the Hybrid Coordinate Ocean Model (HYCOM) to study the dispersion of green turtles from various rookeries within our study region (Putman & Naro-Maciel, 2013). Hatchlings within each of the three distinct hatchling dispersion zones we identified (Figure 2) would be exposed to different oceanic conditions and threats. For example, within the Gulf of Guinea, the threats turtles face from certain anthropogenic activities such as pelagic longline fisheries are apparently lower than in the offshore dispersion zones (Fossette et al., 2014), whilst threats from coastal fisheries and plastic entanglement/ingestion are anticipated to be higher (Schuyler et al., 2015). Within our study region, chlorophyll levels were highest within the Gulf of Guinea, near the African and Brazilian coasts and across a large offshore region along the equator (Figure 2f). The two major offshore dispersion areas identified from our model drift simulations bordered this highly productive equatorial zone to the North and South. Whilst data on the distribution and abundance of the gelatinous organisms leatherback turtles prey upon are sparse (Witt et al., 2007), chlorophyll concentrations are commonly used as a proxy for prey abundance and foraging adult turtles are known to exploit regions of high productivity (Block et al., 2011; Witt et al., 2011). It is unclear whether regions of such high primary productivity are a requirement for, or good indicators of, the habitats used by small juvenile sea turtles; however, larger juvenile turtles (60–100 cm SCL) encountered as bycatch were found in this productive central offshore zone (Huang, 2015) and some satellite-tracked post-breeding adult sea turtles from Gabon also utilised this region (Witt et al., 2011). Nevertheless, whilst the swimming behaviours of juvenile leatherback turtles are largely unknown, their at-sea distributions will be shaped by both active and passive movements (e.g., Gaspar et al., 2012; Putman & Mansfield, 2015; Putman, Scott, et al., 2012; Putman, Verley, et al., 2012; Scott, Marsh, & Hays, 2012b). As hatchling turtles are known to embark on periods of directional swimming that can help them reach favourable habitats (e.g., Lohmann, Cain, Dodge, & Lohmann, 2001; Scott, Biastoch, et al., 2014; Wyneken & Salmon, 1992), our simulated

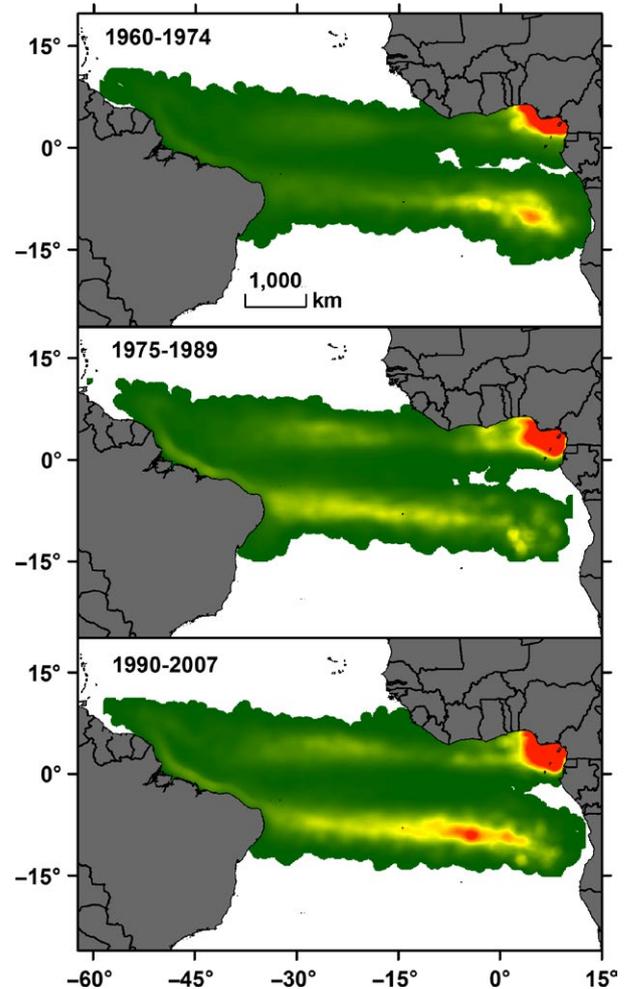
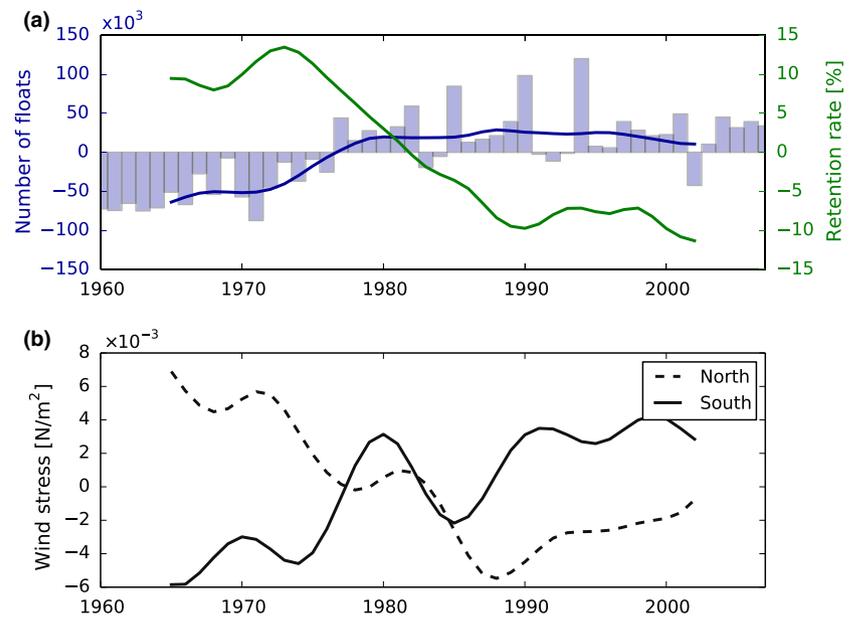


FIGURE 3 Temporal variation in dispersion patterns. The dispersion densities of hatchlings from highest to lowest density (red to green) from Gabon are plotted based on their locations after 6 months of drift for each time period (1960–1974, 1975–1989 and 1990–2007). Dispersion statistics are weighted to reflect differences in nesting densities between northern, central and southern Gabon (Witt et al., 2009)

hatchlings could enter this more productive central zone should it afford better development conditions.

In addition to spatial variability, temporal variability in hatchling dispersion scenarios was high, which is to be expected in a dynamic equatorial region. In the Northern Hemisphere and Southern Hemisphere, geostrophic circulation dominates due to the Coriolis force (a result of the Earth's rotation) and the resultant deflection of ocean currents/winds in either a clockwise/anticlockwise direction, respectively. However, at the equator, the Coriolis force goes to zero, current flows move zonally from areas of high to low pressure and ageostrophic currents dominate (such as those associated with instabilities in the mean flow and frictional effects such as Ekman drift). Trade winds also converge at the equator to form the ITCZ, a key component of both the global climate system and local seasonal variations as it shifts 5–10° north and south each year. As the ITCZ moves from south to north (from January to July/August),

FIGURE 4 Long term Inter-annual variability in hatchling dispersal and oceanic conditions. Top panel: Yearly averages of the number of floats that propagated west of 10°W after 6 months of drift (bar plot) are depicted alongside low pass filtered signals of the retention rates of floats within the Gulf of Guinea (green line) and float numbers that propagate west of 10 °W (blue). Bottom panel: The low pass filtered signals of wind stress magnitude north and south of the equator (solid black and dashed blank lines respectively) are plotted. All quantities are given as anomalies with respect to the overall mean.



wind stress magnitude increases in our study region and hatchlings south of the equator have a higher potential to disperse offshore the later they emerge during the hatchling season (Table S1; Figure S2). Over the last five decades, decadal trends in variability in wind stress magnitude resulted in a trend for an increased rate in the proportion of floats that propagated west and into the South Atlantic Ocean and decreased rates of floats that were retrained in the Gulf of Guinea (Figures 3 and 4). Previous assessments into hatchling dispersal were based on ocean model simulations over much shorter time periods (≤ 1 decade; e.g., Gaspar et al., 2012; Godley et al., 2010; Putman, Scott, et al., 2012; Putman, Verley, et al., 2012; Scott et al., 2012b; Scott, Marsh, et al., 2014; Shillinger et al., 2012) and only very recently has hatchling drift been studied over several decades (Ascani et al., 2016). Ascani et al. (2016) highlighted that even subtle changes in relatively stable oceanic conditions can have important influences on the dynamics of sea turtle populations. In our study region, temporal variation in ocean-mediated hatchling dispersion patterns were particularly high further highlighting the importance of long time series when dealing with dynamic oceanic regions and large-scale oceanic processes and trends which are decadal in nature.

Any shift in hatchling development habitats arising from spatio-temporal variability in oceanic conditions has important implications as different habitats will expose hatchlings to different threats and environmental conditions (such as sea surface temperatures) which will affect life history attributes such as growth and survival rates (e.g., Patrício, Diez, & van Dam, 2014). These implications are anticipated to influence important population level characteristics into adulthood such as the size/age structure and dynamics of breeding populations (e.g., Ascani et al., 2016). Intra-/interspecific population differences in foraging habitat selections of adult turtles influence internesting intervals and size/age at maturity as the rate at which turtles can assimilate energy varies between foraging habitats due to differences in oceanic conditions, prey availability and associated migration costs (e.g.,

Broderick, Godley, & Hays, 2001; Hawkes et al., 2006; Hays & Scott, 2013; Saba, Spotila, Chavez, & Musick, 2008; Zbinden et al., 2011). Furthermore, whilst adult sea turtles are powerful swimmers that can travel counter to strong oceanic current flows (e.g., Luschi, Hays, & Papi, 2003), it has been hypothesised that adult hard shelled sea turtles tend to migrate to foraging habitats they previously encountered as juveniles (Hays et al., 2010; Scott, Marsh, et al., 2014). For Central West African leatherback turtle populations, the observed and predicted distributions of small juvenile sea turtles were confined to warmer waters ($\geq 26^\circ\text{C}$ SST) in the north of the South Atlantic Ocean basin, whilst the majority of adult turtles from Gabon migrated to cooler southerly regions of high productivity around the southern African and Brazilian coasts (Witt et al., 2011). Nevertheless, for those that do reach the Brazilian coast within 6 months of drift, they can then drift south with the Brazil current to more southerly foraging habitats exploited by some adults (e.g., see Scott, Marsh, et al., 2014; Scott, Biastoch, et al., 2014 Appendix A). Disparate conservation initiatives are thus required to protect sea turtles throughout different life stages.

To protect highly mobile endangered species knowledge of their movements, behaviours, habitats and threats are a vital prerequisite. In Gabon, data on the movements of adult turtles through local waters recently contributed towards the design of what will become Africa's largest network of Marine Protected areas (Maxwell et al., 2011; Witt et al., 2008); however, the lack of knowledge surrounding juvenile life stages hinders conservation efforts. Ocean models are thus a valuable tool for studying cryptic juvenile life stages because direct assessments of their dispersion routes (e.g., genetic assessments of the origin of turtles caught as bycatch: Monzon Arguello et al. 2010) are very scarce. Nevertheless, in the light of significant improvements in the ability to rear leatherback hatchlings in captivity (e.g., Jones et al., 2011) alongside recent advances in the miniaturisation of acoustic tracking devices now small enough to actively track hatchlings after they first enter the sea (Scott, Biastoch, et al., 2014; Thums et al., 2016), key knowledge gaps need to be addressed surrounding

hatchling swimming behaviours. Ultimately, the integration of accurate swimming behaviour data into Lagrangian simulations coupled with in situ oceanographic data collection and hatchling tracking studies are now key to improving the realism of dispersal simulations. Until then, it is clear that due to the dynamic nature of marine ecosystems, careful consideration into local oceanic conditions and the relevance of different temporal and spatial scales is required to help inform studies into and the management of endangered marine populations. In particular, spatial and temporal variability in local oceanic conditions should be taken into consideration within regional management units established to help manage sea turtle populations globally (Wallace et al., 2010). Indeed, the significant differences in dispersion scenarios between the main nesting sites in the North and South of Gabon highlight the need for subregional management considerations within the world's largest nesting rookery.

AUTHOR CONTRIBUTIONS

Rebecca Scott conceived and lead this manuscript. **Arne Biastoch**, **Patrick Wagner**, **Till Bayer** and **Franziska U. Schwarzkopf** provided oceanographic input/expertise; **Matthew J. Witt**, **Brendan J. Godley**, **Angela Formia**, **Pierre D. Agamboue**, **Francois L. Boussamba**, **Brice D. K. Mabert**, **Jean C. Manfoumbi** and **Guy-Philippe Sounguet** provided biological input (e.g. satellite tracking data) and/or assisted with fieldwork to satellite track adult leatherback sea turtles from Gabon. The Government of Gabon and the Agence Nationale des Parcs Nationaux granted authorisations and support and Aventures Sans Frontières and the Gabon Sea Turtle Partnership provided field assistance.

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BIOSKETCH

Rebecca Scott is a sea turtle specialist whose research focuses on the use of novel interdisciplinary approaches (particularly the combination of oceanographic and new animal tracking technologies) to study the ontogeny of the cryptic in-water behaviours and movement patterns of sea turtles from hatchlings into adulthood. Rebecca Scott conceived this research whilst based at the GEOMAR Helmholtz Centre for Ocean Research in Kiel and funded by grants (CP1217, CP1502 and CP1625) from the Cluster of Excellence 80: “The Future Ocean”. “The Future Ocean” is funded within the framework of the Excellence Initiative by the Deutsche Forschungsgemeinschaft (DFG) on behalf of the German federal and state governments. TRATL01 was developed within the DFG project SFB754 and integrated at the North-German Supercomputing Alliance (HLRN). The Natural Environment Research Council (NE/J012319/1), The Marine Turtle Conservation Fund (United States Fish and Wildlife Service, U.S. Department of the Interior), Vaalco Energy and Harvest Natural Resources funded satellite tracking work.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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