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Identifying global favourable habitat for early juvenile loggerhead sea turtles

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Loggerhead sea turtles (*Caretta caretta*) nest globally on sandy beaches, with hatchlings dispersing into the open ocean. Where these juveniles go and what habitat they rely on remains a critical research question for informing conservation priorities. Here a high-resolution Earth system model is used to determine the biophysical geography of favourable ocean habitat for loggerhead sea turtles globally during their first year of life on the basis of ocean current transport, thermal constraints and food availability (defined here as the summed lower trophic level carbon biomass). Dispersal is simulated from eight major nesting sites distributed across the globe in four representative years using particle tracking. Dispersal densities are identified for all turtles, and for the top 15% 'best-fed' turtles that have not encountered metabolically unfavourable temperatures. We find that, globally, rookeries are positioned to disperse to regions where the lower trophic biomass is greatest within loggerheads' thermal range. Six out of the eight nesting sites are associated with strong coastal boundary currents that rapidly transport hatchlings to subtropical–subpolar gyre boundaries; narrow spatial migratory corridors exist for 'best-fed' turtles associated with these sites. Two other rookeries are located in exceptionally high-biomass tropical regions fuelled by natural iron fertilization. 'Best-fed' turtles tend to be associated with lower temperatures, highlighting the inverse relationship between temperature and lower trophic biomass. The annual mean isotherms between 20°C and the thermal tolerance of juvenile loggerheads are a rough proxy for favourable habitat for loggerheads from rookeries associated with boundary currents. Our results can be used to constrain regions for conservation efforts for each subpopulation, and better identify foraging habitat for this critical early life stage.

1. Introduction

Conservation of migratory marine animals presents a number of challenges owing to their complex life cycles, vast distances travelled and the difficulty of obtaining information on their spatio-temporal distributions. Sea turtles epitomize this problem; like many migratory marine vertebrates, the majority of sea turtle species are endangered or threatened (e.g. [1]). Loggerhead sea turtles (*Caretta caretta*) nest on sandy beaches from temperate to tropical latitudes; upon hatching they migrate offshore to escape the heavy predation that occurs in coastal waters (e.g. [2,3]). Small loggerheads spend five or more years in the open ocean before returning to coastal habitats; upon reaching maturity one to three decades later, they largely

Table 1. Simulated loggerhead rookeries, including location and hatching season. Sites are plotted in figure 1.

site no.	location	latitude	longitude	hatching season
1	Japan	30.3	130.5	15 July–15 Oct
2	Florida	25.9	−80.1	1 July–30 Sep
3	Cape Verde	16.1	−22.9	1 Sep– 30 Nov
4	Oman	20.3	58.7	1 Apr–30 Jun
5	west Australia	−25.8	113	1 Jan–30 Mar
6	east Australia	−24.7	152.4	1 Jan–30 Mar
7	Brazil	−12.7	−37.9	1 Dec–30 Mar
8	South Africa	−27.4	32.7	1 Jan–30 Mar

return to the vicinity of their natal site to reproduce (e.g. [4]). While conservation efforts have led to increases in nesting for several populations in recent decades [5], many remain threatened or endangered [6]. Key questions about turtle life histories needed to inform conservation efforts, and in particular our ability to predict climate change impacts, remain unanswered [1,6–10]. Because sea turtle population abundance appears to be strongly related to the successful dispersal from nesting beaches to oceanic habitats [11,12], one of the most important questions is the dispersal fate of hatchlings from natal beaches in their first year of life [13].

Early juvenile turtle dispersal is termed the ‘lost years’, owing to the post-hatchling disappearance of juveniles from coastal waters where they are easily observed [14,15]. There are many critical gaps in our understanding of the biogeography of sea turtles in early juvenile stages, including: identifying key pelagic foraging habitats, what parameters delineate and control spatio-temporal variation in pelagic habitats and how nesting sites connect to these foraging grounds [1,10]. Turtle hatchlings are difficult to observe owing to their small size, rapid growth rates and high mortality; because of weight constraints, satellite tracking only becomes feasible when they are many months old [16–19]. While genetic studies have made great advances in understanding the connection between rookeries and late-juvenile foraging grounds [20,21], details of where hatchlings go in the first year and what pelagic habitat they rely on remain elusive. Understanding the connection between rookeries and favourable pelagic habitat is critical for managing this most enigmatic life stage, and it is here that ocean models have great utility.

Ocean models are increasingly being used to support and inform turtle management and *in situ* studies. Particle tracking, following simulated water trajectories through time, either as passive transport or with biologically motivated simulated swimming, has been used to model the movements of a number of sea turtle species at different life stages across various ocean basins to answer a variety of research questions (e.g. [13,22–28]). Modelling particle trajectories requires ocean velocity representation of mesoscale (10–100 km) features such as jets and eddies that are integral to dispersal [29,30]. However, physics-only ocean models do not represent the limitations on oceanic habitat due to food availability, necessitating models that include ocean ecosystem simulation. Running eddy-resolving simulations at the global scale with ocean biogeochemistry is computationally expensive; such simulations are just beginning to be used for biogeochemical and ecological research (e.g. [31–34]).

The goal of this study is to examine loggerhead dispersal from eight major nesting sites across the globe [35,36] and identify key pelagic habitat for juveniles in their first year based on: (i) transport of turtles by ocean currents, (ii) sea surface temperatures (SSTs) within a physiologically acceptable range, and (iii) likely food availability for turtles. For the first time, we use a global high-resolution Earth system model with ocean biogeochemistry to simulate global loggerhead juvenile dispersal and the along-path food availability. We estimate food availability for juvenile loggerheads along their dispersal paths by summing phytoplankton and zooplankton biomass fields in the model, termed ‘bioC’ (see Methods). This methodology allows us to simulate where turtles with the greatest foraging opportunities within a favourable thermal range are likely to be concentrated during their first year, and thus what oceanographic conditions should contribute to increased fitness for loggerheads during the ‘lost years’.

2. Methods

Hatchling dispersal was simulated from eight loggerhead nesting sites distributed globally (table 1 and figure 1), by selecting the site with the largest nesting abundance within each region [5,36]. The Mediterranean Sea was excluded owing to poor representation in the global ocean model. Particles representing hatchling turtles were released over the hatching season (lasting 3–4 months) from each nesting location (table 1) on a regular 0.1° grid, extending in a 1° box centred on the nesting beach. This initial wide horizontal spread is intended to account for offshore directed swimming during the initial post-hatching ‘frenzy’ period [24,37]. Particles were released throughout the hatching season for each site (table 1), resulting in approximately 2500 particles released each year from each site, with variation due to the different hatching season durations and coastline orientations.

Hatchlings were simulated over the first year as passive particles, assuming that after an initial post-hatching frenzy period they are passively carried by ocean surface currents. Although models indicate that swimming behaviour can substantially contribute to net movement and the processes influenced by it (e.g. mortality, growth rates, distribution, etc. [22–24,28,38–40]), our aim in this study was to identify ‘optimal habitat’; that is, locations that are highly productive and require no (or very little) energetic cost to reach. Such an approach is useful for producing a ‘null hypothesis’ for the distribution of marine organisms and shows how ocean current transport contributes to observed spatio-temporal variation in the distribution and abundance of sea turtles [41–43].

Ecological dispersal simulations use ocean velocity field data from an ocean model or remote sensing product, combined with

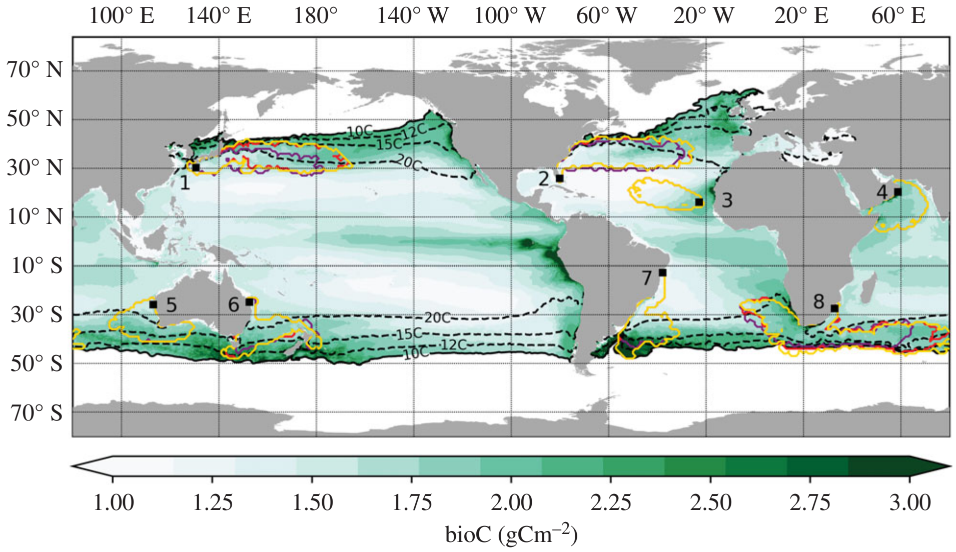

Figure 1. Loggerhead rookeries, simulated mean ocean conditions and favourable pelagic habitat. Simulated rookeries (black squares; table 1); annual mean total planktonic biological carbon biomass (bioC; colourmap) within loggerhead thermal limits; annual mean SST isotherms (black lines), with the 10°C isotherm highlighted (solid black line), representing the lowest thermal tolerance assumed for loggerhead hatchlings. Overlaid are 'best-fed' dispersal envelopes for the 10°C (orange), 12°C (red) and 15°C (purple) thermal thresholds. For some sites, there is no or little change in dispersal with the changing thermal threshold (table 2). Note that turtle dispersal is simulated in the time-varying ocean, so that dispersal envelopes may exceed the annual mean isotherms.

a particle integration model that tracks where the organism in question is transported by these velocities. Here velocities were taken from a high-resolution (0.1°, nominally 10 km) global ocean simulation with biogeochemistry, the Community Earth System Model with Biogeochemical Elemental Cycling (CESM-BEC). This ocean model simulation was forced by the Coordinated Ocean-Ice Reference Experiments (CORE-I) 'normal year' dataset [44], such that the atmospheric forcing fields repeated each year and variability is entirely internal to the ocean (eddy variability). The BEC ecosystem model includes three phytoplankton functional types (small phytoplankton, diatoms and diazotrophs) and one zooplankton functional type, as is common for Earth system models (e.g. [33,45]). The horizontal model resolution is eddy resolving globally, the state of the art for computationally expensive global biogeochemically enabled models (e.g. [31,33]). The ocean model simulation was run for 5 years, with average history files written every 5 days. The CESM-BEC model has been extensively validated with global productivity, export and biogeochemical patterns (e.g. [46]). The high-resolution CESM ocean simulation used here compares well with observations of physical parameters such as temperature (electronic supplementary material, figure S1), observed eddy tracks [47] and biological parameters such as chlorophyll [32,33], and net primary productivity (NPP; model compared with satellite-derived NPP in electronic supplementary material, figure S2).

Virtual loggerhead hatchlings (particles) were released at the same frequency as the ocean model velocity output, every 5 days, during each hatching season over the ocean model run, resulting in four 1-year hatchling simulations for each nesting site. The Connectivity Modelling System (CMS; [48]) was used to integrate particle trajectories using the simulated ocean surface velocities and modified to save food proxies from CESM-BEC, interpolated daily along the trajectory paths, along with ocean SST. CMS interpolates the ocean velocity, temperature and food proxies in space and time and integrates particle trajectories using standard methods, bilinear for interpolation and fourth-order Runge–Kutta for integration [48], and has been used extensively in a wide range of dispersal studies (e.g. [49–51]).

Loggerhead turtles are poikilothermic, with only a small ability to regulate their internal body temperature, such that water temperatures below around 10–15°C are metabolically unfavourable; older juveniles and adults are largely observed in much warmer waters [25,52–54], while hatchlings behave normally in waters as cold as 9°C [55,56]. Trajectories that passed into regions where the SST was less than 10°C were retained in the main sample, to provide an indication of where hatchlings may be carried, but were considered 'frozen', i.e. outside of their thermal tolerance limit, and excluded from the subsample of 'best-fed' trajectories (see below). Sensitivity analyses were conducted in which this thermal threshold was also considered at 12°C and 15°C. Particles that beached (i.e. stranded) at any time during the first year were considered unsuccessful and not analysed. This treatment of beached particles accounts for the limited potential for small turtles to survive in near-shore waters. The number of particles excluded owing to temperature exposure and stranding varied from site to site, and was often significant, such that the total number of trajectories analysed from each site for the 10°C threshold was reduced to between 1000 and 6000 total over the 4 years. Sensitivity tests releasing more particles did not significantly change our results.

Representing global prey distributions for sea turtles is challenging. Loggerhead juveniles are observed to have a diverse diet heavy on gelatinous zooplankton (e.g. [57]), feeding at trophic levels not well observed or currently represented in most Earth system models [58]. Models of NPP based on satellite observations of ocean colour represent the rate of carbon fixation by phytoplankton per unit area, i.e. phytoplankton production (see electronic supplementary material, figure S2; e.g. [59,60]). These NPP estimates have often been used as a food proxy in turtle studies; in terms of observation-based estimates, NPP is arguably the best available for sea turtle food abundance, as meso-zooplankton and gelatinous zooplankton observations are fairly sparse [61,62]. However, turtles eat biomass and not the phytoplankton production represented by NPP, production which is often quickly recycled and not translated into increased biomass. Using the Earth system model biogeochemical output, we are not limited to observational measures such as NPP as a food proxy source, and so we constructed a metric that better captures the ability of regional ocean ecosystems to generate and retain biomass, bioC, the total carbon biomass of all simulated phytoplankton and zooplankton (units of gCm^{-2}). For the sake of completeness, we have also included some evaluation of the model skill in reproducing observed NPP patterns.

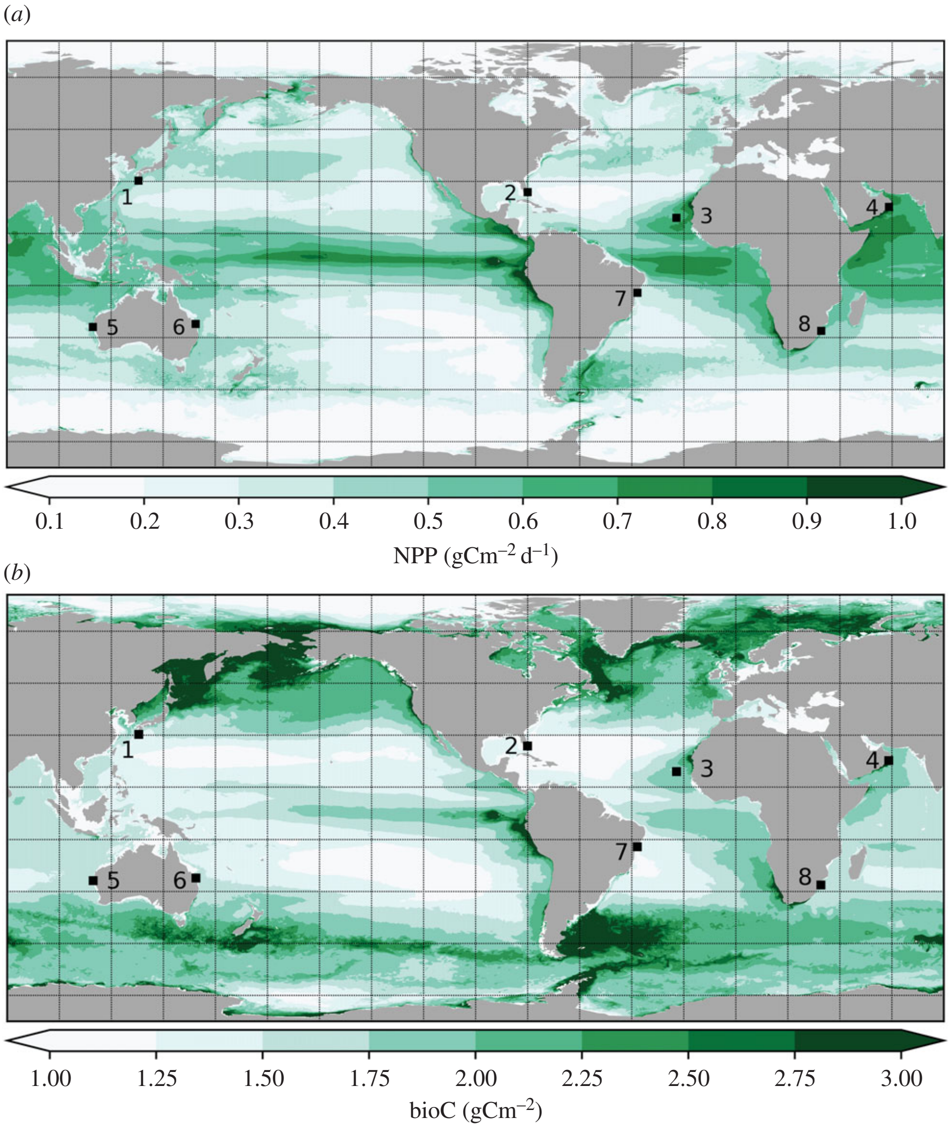

Figure 2. (*a*) Simulated annual mean net primary productivity (NPP), and (*b*) total depth-integrated planktonic carbon biomass (bioC), shown at model resolution (approx. 0.1°). NPP is higher in tropical biomes, while bioC is greatest at high latitudes.

Total plankton carbon biomass (bioC) and NPP have distinct spatio-temporal structures (figure 2; electronic supplementary material, movie). Globally, annual mean NPP is highest in small phytoplankton-dominated tropical regions that have lower zooplankton biomass and bioC than higher latitude systems. These highly recycling biomes have low trophic efficiency, leading to low biomass and low abundance at mid-trophic levels, and thus low forage for higher trophic levels, making NPP a poor proxy for loggerhead food availability. By contrast, mean NPP is relatively low in subpolar regions (poleward of approximately 40°), while biomass is high, resulting from increased phyto- to zooplankton trophic efficiency in the colder, more nutrient-rich waters and large standing stocks of zooplankton throughout the year [60,63]. Here again NPP is not a good indication of potential food biomass. Validation data for biomass are limited, but we note that zooplankton biomass, as represented in the COPEPOD database (https://www.st.nmfs.noaa.gov/copepod/), has similarly high values to bioC in subpolar biomes [61,63].

To visualize the dispersal of those loggerheads that have the highest probability of survival after the first year, we constructed dispersal distributions for 'best-fed' juveniles. For this, we assumed that fitness is cumulative, determined by the sum of food availability (bioC) along the turtles' trajectory for the first year. From these distributions, we designated the top 15% from the cumulative food availability as 'best-fed'. The impact of thermal threshold on 'best-fed' dispersal distribution median values was tested using an ANOVA over the 4 years for each site.

2.1. Model limitations

The global model used here, while state of the art, has biases pertinent to our findings. The Gulf Stream, Kuroshio and Agulhas retroflection currents are too far poleward, seen as a warm winter SST bias in electronic supplementary material, figure S1, a common bias for western boundary currents (WBCs) [64,65], and are associated in this simulation with an approximately 2° C cold bias on their poleward side (electronic supplementary material, figure S1). This likely affects our estimates of juveniles encountering cold temperatures and suggests our simulated cold thermal threshold of 10°C could be closer to 12°C for the *in situ* temperatures of the poleward flank of these boundary currents. Further observational and better validated regional modelling studies are needed for accurate assessment of these gyre boundaries in relation to turtle habitat suitability.

Even at 10 km resolution, coastal physical processes controlling dispersal and nutrient delivery are poorly represented, as they are mediated by very near-shore circulation and wind structure not resolved here [58,66,67], thus we have restricted our analysis to non-beached hatchlings and parameterized the frenzy swimming period instead of simulating it directly. Additionally, river nutrient fluxes, similar to other Intergovernmental Panel on Climate Change class Coupled Model Intercomparison Project Phase 5 (CMIP5) models [68], are not simulated. The result of these missing nutrient sources is a low-productivity model bias in coastal regions where river nutrients (e.g. Amazon, Mississippi) and upwelling (e.g. eastern South Atlantic) sources are important (electronic supplementary material, figure S2). We note that the model agrees well with observation-based productivity estimates off-shelf (electronic supplementary material, figure S2), so that the pelagic favourable turtle habitat found here should be quite robust. Since loggerhead hatchlings are observed to rapidly swim offshore to leave coastal waters, a behaviour that is likely to reduce predation risk [69], on-shelf productivity is arguably not the most important factor controlling their survival in the first year.

3. Results and discussion

3.1. Oceanographic geography of loggerhead nesting sites

A priori, simulated rookery locations do not appear favourable with respect to food availability for oceanic-stage hatchlings (figure 1). The majority are positioned near oligotrophic gyres where plankton biomass is globally lowest (figure 2*b*), and hatchlings are observed to quickly leave productive coastal waters, where predation is thought to be highest (e.g. [14]). Instead of relying on local food availability, we find that the location of many loggerhead nesting sites facilitates the dispersal of hatchlings towards high-biomass regions (figures 1 and 3). While it has long been noted that major loggerhead nesting sites are associated with boundary currents [11,70], here we can provide a mechanistic context combining transport and food availability to explain this association.

Five of the eight loggerhead nesting sites simulated are associated with major WBCs: the Kuroshio (site 1), Gulf Stream (site 2), East Australian (site 6), Brazil (site 7) and Agulhas Currents (site 8). These nesting sites are located inshore of low-production subtropical gyres; WBCs move hatchlings rapidly poleward and into the productive subtropical–subpolar gyre boundaries, where biomass is the highest within loggerheads' thermal range (figure 1). Every major WBC has a loggerhead nesting beach in a similar oceanographic setting: on the western flank of the poleward-flowing current where it is closest to shore, optimally placed for rapid advection to these gyre boundaries, and these nesting sites represent the most successful in each WBC region. A sixth nesting site is associated with the Leeuwin Current off west Australia (site 5), a singular eastern boundary current in that it is poleward flowing instead of equatorward, owing to strong onshore flow, which limits upwelling (e.g. [26,71]). Thus, the Leeuwin functions much like a WBC, moving hatchlings poleward into more productive, high-biomass subantarctic waters (figure 1; [26]). Additionally, the Oman site (site 4) is associated with the Arabian Current, a relatively weak boundary current that transports hatchlings out of the near-shore and into the Arabian Sea during their first few weeks (figures 1 and 2*b*).

While the WBC nesting sites disperse to regions of high food abundance, risk of exposure to cold, metabolically unfavourable temperatures can be high (table 2 and figure 1). In this simulation, Japan and Florida have the highest rate of exposure to temperatures below 10°C, ranging between 40–58% and 36–59%, respectively, with interannual differences driven by eddy variability. When hatchlings are restricted to warmer thermal thresholds, the proportion of cold-stressed hatchlings increases to 67–77% and 44–67% for 12°C and to 87–94% and 73–84% for 15°C, respectively. Similarly, while simulated cold exposure is low for the South African rookery at 10°C (3–9%), it more than triples for 12°C (22–33%), and doubles again for 15°C (50–62%). Other boundary current associated nesting sites, such as Brazil and east Australia, have no exposure to temperatures below 10°C, and very little danger of thermal stress at warmer thresholds (0–5% at 15°C). The two tropical sites in Oman and Cape Verde Islands, along with the western Australian rookery, have no thermal limitation at any threshold.

The two tropical sites not associated with major boundary currents, Cape Verde Islands (site 3) and Oman (site 4), are similar in that they feature high food abundance, warm temperatures over the first year and low or moderate dispersal distances over the first year (table 2 and figure 4). These nesting sites are located in regions with exceptionally high biomass for tropical waters (figure 1), such that integrated biomass is as high as or higher than that for many of the boundary current associated sites over the first year (table 2 and figure 4). Exceptional productivity in these two regions is driven by a combination of Aeolian iron fertilization and coastal upwelling [72,73].

3.2. Ocean biophysical constraints on hatchling foraging success

Dispersal distributions of simulated turtles in the top 15% of along-track integrated biomass, labelled here as 'best-fed', depict where pelagic habitat is most favourable for the juveniles (figures 1 and 3*b*). The difference between 'best-fed' and total dispersal distributions varies by nesting site (figure 3). From low-dispersal tropical sites (sites 3 and 4), the 'best-fed' distributions are more similar to the total dispersal distributions (figure 3*a*), following the spatially and temporally consistent high food abundance near these rookeries. For nesting sites associated with boundary currents, 'best-fed' distributions are predominantly skewed poleward, towards higher food biomass at the subtropical–subpolar gyre boundaries and away from the centres of oligotrophic subtropical gyres.

'Best-fed' distributions have significantly different temperatures relative to total dispersal distributions ($p < 0.05$ in all sites using a Kolmogorov–Smirnov test with 100 bootstrapped samples from the 'best-fed' trajectories and from all trajectories; figure 4). For the 10°C thermal threshold, six sites have significantly cooler 'best-fed' distributions, highlighting the correlation of cool waters, upwelling-driven nutrient availability and food abundance. For example, despite the large overlap in total and 'best-fed' distributions, the 'best-fed' turtles from Oman (site 4) spend more time in the western and central Arabian Sea (figure 3), where upwelling and monsoon-driven vertical mixing provide higher productivity, along with cooler temperatures [74,75]. Florida and Japan have significantly warmer distributions for 'best-fed' turtles than all releases (figure 4*b*). Both of these nesting sites are subject to high rates of encountering temperatures below 10°C (table 2), constraining the 'best-fed' distributions to warmer waters.

The impact of changing the thermal tolerance on the 'best-fed' distributions depends on the nesting site and the

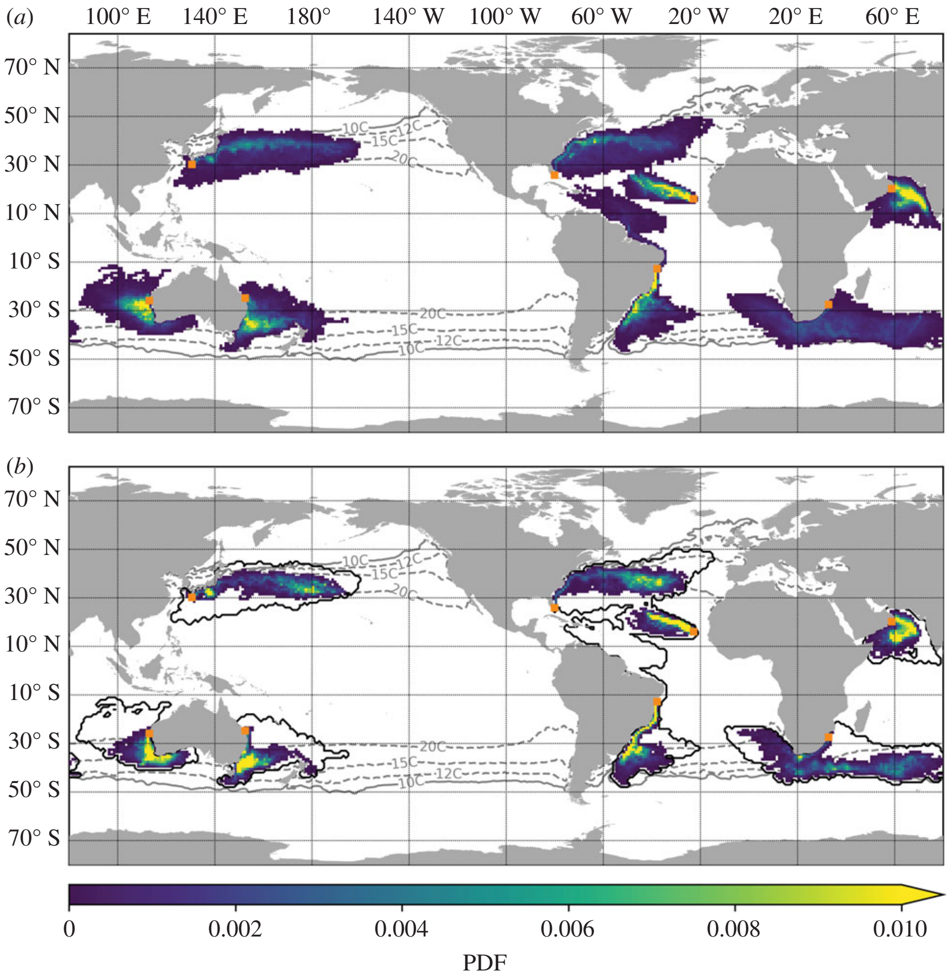

Figure 3. Simulated loggerhead dispersal. (*a*) Two-dimensional probability distribution functions (PDF) of dispersal (colourmaps) from each rookery (orange squares) for all non-stranded particles. (*b*) 'Best-fed' (top 15%) dispersal distributions, which exclude simulated hatchlings that have encountered temperatures less than 10°C; extent of total dispersal (black contours) is shown for comparison. Annual mean isotherms (grey) as in figure 1. 'Best-fed' dispersal envelopes for the 12°C and 15°C thermal thresholds are shown in figure 1 and the probability distributions in electronic supplementary material, figure S3.

magnitude of the thermal threshold (table 3, figures 1, 4 and 5 and electronic supplementary material, figure S3). With all thermal thresholds, there is no impact on 'best-fed' distributions for the two tropical nesting sites (table 3, figures 1, 4 and 5), as simulated encounter temperatures for Oman and the Cape Verde Islands are always well above 20°C (figure 4*b*). Additionally, the 'best-fed' dispersal distributions for the two Australian and the Brazil sites do not significantly depend on temperature (ANOVA, $F_{2,3} < 17$, $p > 0.05$ for all three sites). Using a 15°C thermal threshold significantly affects the 'best-fed' dispersal distributions, in both latitude and longitude, for the Japan, Florida and South Africa nesting sites (ANOVA, $F_{2,3} > 17$, $p < 0.05$ for all sites; table 3 and figure 5). For the Japan release site and a 15°C thermal threshold, a large proportion of 'best-fed' hatchlings are retained in a persistent Kuroshio meander off the Japanese coast (electronic supplementary material, figure S3b), resulting in the dispersal envelope median shifting over 20° westward (table 3 and figure 5) and reducing the median dispersal distance by over 1000 km (figure 4*c*). The Florida 'best-fed' dispersal distribution for 15°C is also shifted west and south (figure 5; electronic supplementary material, figure S3), resulting in reduced dispersal distance (figure 4*c*). For the South African site, the 15°C 'best-fed' dispersal median moves over 20° west (table 3) and from the Indian to the Atlantic Ocean (figure 5). For all of these last three sites, the restriction to warmer waters leads to a decrease in food exposure for 'best-fed' hatchlings over the first year (figure 4). Changing the thermal threshold from 10°C to 12°C has less impact for these sites, with a large overlap in the 'best-fed' envelopes (figure 2) and less change in food exposure, mean temperature and distance travelled (figure 4) and median dispersal (table 3 and figure 5).

3.3. Defining global favourable pelagic juvenile loggerhead habitat

A posteriori, favourable pelagic juvenile loggerhead habitat in the first year can be defined by comparing average ocean conditions with 'best-fed' turtle dispersal envelopes (figure 1). Here, we find that rookeries are positioned globally to disperse to the highest biomass regions within loggerheads' thermal range. This is accomplished either by the nesting sites being located in high-biomass regions (sites 3 and 4) or by rapidly dispersing to such regions via boundary currents (all other sites). In the latter case, pelagic favourable habitat can be characterized by isotherms associated with subtropical–subpolar gyre boundaries. The annual mean isotherm range from the loggerhead cold threshold (e.g. 10°C) to 20°C is a good thermal proxy for favourable loggerhead hatchling habitat for all boundary current associated nesting sites, as indicated by the 'best-fed' dispersal envelopes after

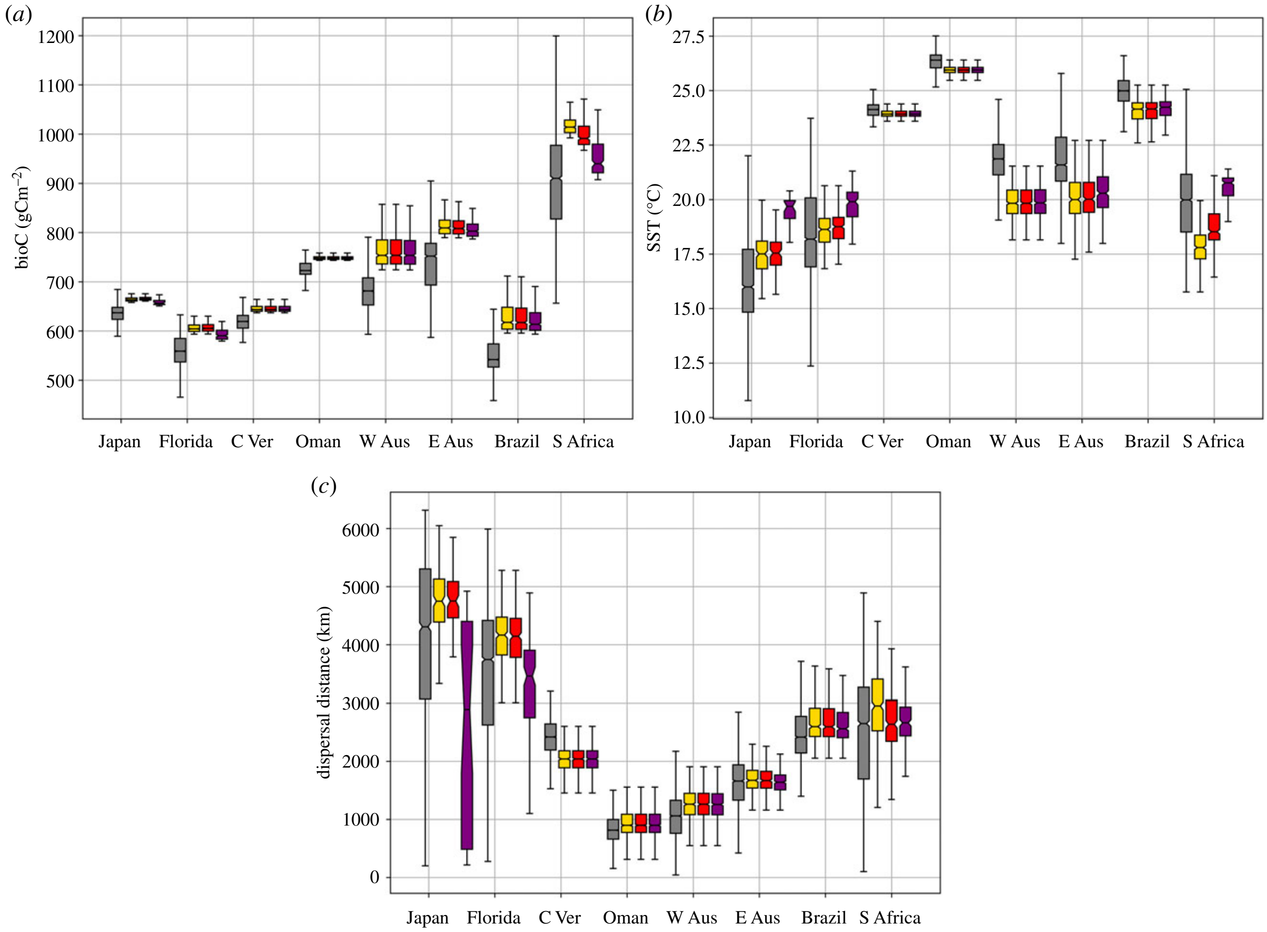

Figure 4. Intersite statistics for (*a*) bioC integrated over the first year, (*b*) average SST over the first year and (*c*) distance from nesting site at the end of the first year. Combined distributions for the four simulation years are shown for all releases (grey), and 'best-fed' distributions at the 10°C (gold), 12°C (red) and 15°C (purple) thermal tolerance thresholds.

Table 2. Summary model results for each nesting site, taken along trajectories for the first year, combining four dispersal years. SST is the median SST across all releases and all times, bioC is the median of the summed along-track lower trophic carbon biomass and distance is the median of the great circle distance from the nesting site at the end of 1 year. Proportion 'frozen' is the per cent of releases that encounter temperatures below the given thermal threshold (10°C, 12°C and 15°C) at any time in the first year, with ranges for interannual variability.

site no.	location	SST (°C)	bioC (gCm^{-2})	distance (km)	proportion 'frozen' (%) for 10°C	proportion 'frozen' (%) for 12°C	proportion 'frozen' (%) for 15°C
1	Japan	16	640	4310	40–58	67–77	87–94
2	Florida	19	560	3740	36–59	44–67	73–84
3	Cape Verde	24	620	2420	0	0	0
4	Oman	26	720	810	0	0	0
5	west Australia	22	680	1060	0	0	0
6	east Australia	22	750	1660	0	0–1	0–5
7	Brazil	26	540	2410	0	0	0–3
8	South Africa	20	910	2650	3–9	22–33	50–62

the initial narrow corridor stage (figure 1). Indeed, the majority of the ocean area with high biomass is associated with waters colder than 20°C.

For any thermal threshold used, the 'best-fed' distributions from boundary current sites are always skewed towards the thermal threshold, where ocean bioC is highest (figures 2 and 5; electronic supplementary material, figure S3). Thus, using a warmer thermal threshold does not modify the main results that favourable pelagic habitat is largely at the subpolar–subtropical gyre boundaries, but simply shifts the favourable habitat equatorward.

Adult loggerheads are usually found in waters above 12°C (e.g. [53,54]), but acclimated adult loggerheads have been observed in much colder waters [52]. Studies have shown that loggerhead juveniles are more cold tolerant than adults, and hatchlings even more so, even without slow acclimation

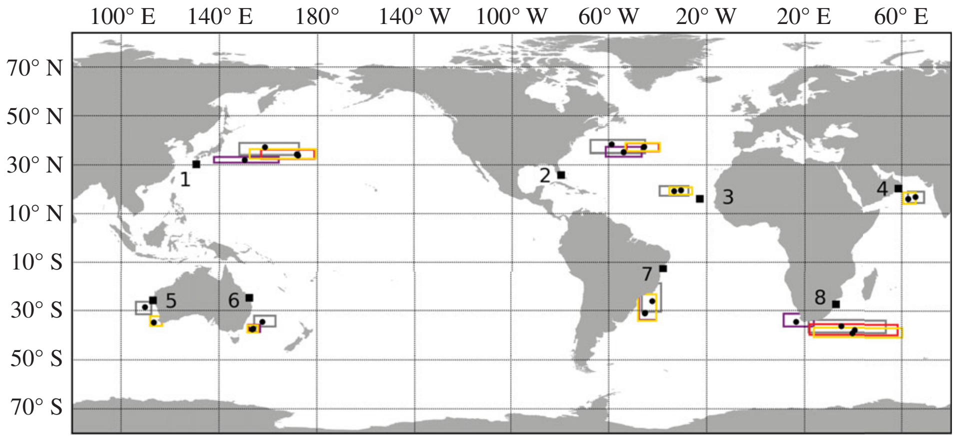

Figure 5. Two-dimensional inter-quartile range plots for total dispersal (grey) and 'best-fed' distributions for the three thermal thresholds: 10°C (gold), 12°C (red) and 15°C (purple). Circles mark median points; see table 3 for median values and significance testing. For Japan (site 1), Florida (site 2) and South Africa (site 8), the thermal threshold significantly affects dispersal (table 3).

Table 3. Two-dimensional median coordinates for dispersal distributions, including all non-stranded hatchlings (total dispersal) and 'best-fed' hatchlings for the three thermal thresholds: 10°C, 12°C and 15°C. Italicized numbers indicate nesting sites where the change in thermal threshold significantly changes the median dispersal (ANOVA, $F_{2,3} > 17$, $p < 0.001$).

site no.	location	total dispersal (lat, lon)	10°C 'best-fed' dispersal (lat, lon)	12°C 'best-fed' dispersal (lat, lon)	15°C 'best-fed' dispersal (lat, lon)
1	Japan	37.1, 158.5	*34.2, 171.5*	*33.9, 172.0*	*32.1, 150.2*
2	Florida	38.3, −58.7	*37.3, −45.5*	*37.1, −45.7*	*35.2, −53.9*
3	Cape Verde	19.3, −33.2	19.6, −30.5	19.6, −30.5	19.6, −30.5
4	Oman	16.79, 65.5	16.1, 62.6	16.1, 62.6	16.1, 62.6
5	west Australia	−28.6, 109.6	−34.9, 113.3	−34.9, 113.4	−34.9, 113.4
6	east Australia	−34.6, 157.6	−37.6, 153.5	−37.6, 153.6	−37.4, 154,0
7	Brazil	−26.2, −42.3	−31.2, −45.3	−31.2, −45.3	−31.1, −45.2
8	South Africa	−36.4, 35.5	*−39.3, 39.6*	*−38.1, 40.6*	*−34.6, 16.6*

[55,56]. Moreover, pelagic-stage juveniles have been shown to use basking and other behavioural strategies that allow them to achieve body temperatures several degrees warmer than SST [17]. Thus, even the lowest threshold for 'freezing' used here (10°C) might be overly conservative, and loggerhead hatchlings may be more tolerant to life at the edge of the subpolar gyres than we assumed. More *in situ* work is needed to assess the relative fitness of young juveniles in these cold regions, and how this changes with size and age.

We note that the annual mean thermal range of less than 20°C indicating favourable habitat is consistent with TURTLEWATCH dynamic ocean management (e.g. [76]) efforts in the North Pacific; the instantaneous 17.5–18.5°C isotherms are used as a benchmark for avoiding fishery interactions with adult loggerheads, constraining certain fishing gear within this thermal range [77]. The less than 20°C range is also consistent with observations of tagged turtle temperature readings and models of habitat suitability in this region [25]. It is interesting to note that the thermal ranges validated in the North Pacific for Japanese loggerheads are extendable globally to other populations associated with boundary currents. The results here suggest that similar management strategies, following the lessons learned in the North Pacific, could be applied globally for minimizing fisheries impacts on juveniles.

Food availability is a critical consideration in determining the favourable pelagic habitat of loggerhead hatchlings. The novelty of this study lies in the inclusion of a food proxy (bioC), computed from outputs of a biogeochemical model, along with physical conditions (SST) in determining favourable habitat. In the Florida and Japan regions, food limitation constrains the 'best-fed' dispersal envelope on the northeastern and southwestern edges to a mostly zonal strip along the gyre boundary. In these areas, food availability serves to concentrate favourable habitat to the centre of the total dispersal distribution. However, in other sites (e.g. Brazil, Australian sites), food limitation reduces habitat wholly on one side (equatorward) of the total dispersal zone; it is clear that assessing favourable habitat based on physical characteristics alone would be insufficient. Despite the coarse food proxy used in this study, our results highlight the importance of including ecosystem variables in assessing pelagic habitat, and that results of this inclusion vary across the rookery sites. As global conservation efforts for large pelagics progress, we suggest that an improved understanding of both the physical and ecological (food web) determinants of favourable habitat is critical for targeting effective action and preserving key ecosystem services.

Young juvenile loggerheads have often been associated with pelagic *Sargassum* algae in the North Atlantic (e.g.

[15]), such that *Sargassum* is used to define critical habitat in US waters [78]. However, *Sargassum* is endemic to the North Atlantic and without parallel in other ocean basins. Though we have not modelled the role of *Sargassum* here, it is likely that high bioC is a necessary condition for early juvenile feeding success and thus fitness globally, whether or not *Sargassum* is present. It is interesting to note that observed and modelled climatologies of *Sargassum* in November [79] are high in the Gulf Stream Extension, across the North Atlantic towards the Azores, in a similar distribution to the 'best-fed' turtles simulated here. This *Sargassum* abundance appears driven by *in situ* growth and not transport [79], suggesting that *Sargassum* is benefiting from the same processes driving high bioC in this simulation.

3.4. Dispersal corridors and endangered populations

Narrow spatial corridors in dispersal pathways are regions of enhanced vulnerability to anthropogenic and environmental stressors, acting as a type of migratory bottleneck (e.g. [80]). 'Best-fed' distributions from boundary current rookeries exhibit these corridors close to the nesting site: narrow regions close to the coast that hatchlings pass through during the first weeks of life (figures 1 and 3). These corridors are associated with the poleward and inshore flanks of WBCs, which disperse these hatchlings to the high-biomass gyre boundaries. Dispersal corridors extend from rookeries to the point where the current detaches from the coast, with significant intersite differences in the length and narrowness (figures 1 and 3*b*). For the Brazil nesting site, this corridor extends from 13° S to 30° S, almost 2000 km, a significant fraction of the median dispersal distance (2410 km; table 2). In other boundary current associated nesting sites, the corridor is of the order of hundreds of kilometres, often extending to 1000 km. In all cases, when narrow dispersal corridors exist, they represent a significant amount of time that expected 'best-fed' hatchlings are in a narrow spatial domain.

The narrow dispersal corridors found for many of the boundary current associated sites suggest a potential vulnerability for loggerhead hatchlings in their very early pelagic stage. Boundary currents are largely associated with the continental shelf break, such that their distance to shore is controlled by shelf width, which varies from basin to basin and along the migratory bottleneck corridor extent for each nesting site. Hatchlings using boundary currents that are closer to the coast could be susceptible to higher rates of natural predation from both aquatic and avian species, as well as anthropogenic stressors such as pollution (e.g. [37,81,82]). Likewise, the length of the corridor will necessarily increase the probability of hatchlings' vulnerability to these threats. These narrow corridors are potentially very fruitful regions for management efforts and could potentially refine management regions currently in use [78].

3.5. Swimming and boundary currents

Within their thermal nesting range, sea turtles typically nest in greatest abundance where passive off-shelf dispersal is optimized, e.g. where boundary currents are closest to shore [11,40]. This is true for seven of the eight loggerhead nesting sites modelled here, as well as Kemp's ridley sea turtle (*Lepidochelys kempii*) [69] and leatherback sea turtles (*Dermochelys coriacea*) [12]. The implications are that proximity to currents favourable for dispersal is a leading-order constraint on nesting habitat for sea turtles in general. Given that fitness is increased for turtles that can reach nursery grounds with limited energy expenditure, and that mature turtles return to the vicinity of their natal site to nest, beaches where hatchling movement is consistently facilitated by ocean currents will tend to have relatively high nesting populations [11]. It also follows that turtle populations nesting at sites less favourable for the transport of hatchlings may undergo strong natural selection for oriented swimming towards these favourable dispersal corridors; evidence strongly suggests that this is the case [37,40,83,84]. Moreover, it is likely that, for all turtle populations, swimming behaviour that increases the chances of young turtles reaching favourable oceanic habitats will be selected for, such as orienting to magnetic map cues [38,85]. A tracking experiment of less than 1-year-old loggerheads from Brazil and simultaneously deployed drifters indicated that large-scale patterns in movements followed the prevailing direction of current flow and that oriented swimming helped turtles maintain their position within currents [86]. Similarly, a tracking experiment with wild-caught, 1- to 2-year-old Kemp's ridley and green sea turtles (*Chelonia mydas*) indicated that oriented swimming behaviour contributed significantly to their movements and habitat selection in the Gulf of Mexico [87]. Accounting for such behaviour in our model would probably not change the favourable habitat regions found here, but increase the overall fraction of hatchlings reaching this favourable habitat [22,40].

3.6. Relative nesting site success

Some combination of suitable nesting conditions and post-hatchling survivability necessarily controls which nesting beaches are the most successful [35,88]. Here, no significant correlation was found between estimated nest abundance (e.g. [6,35,89]) and food proxies, median SST or dispersal distance (Pearson's $r < 0.6$, $p > 0.1$, $n = 8$, for each metric). For example, the two sites with the highest modelled bioC over the first year (South Africa, site 8, and east Australia, site 6; table 2) have estimated nesting populations one or two orders of magnitude lower than Oman or Florida [6,35], with temperature and dispersal distance in the middle range of all nesting sites. These results suggest that other controlling factors are more important for nesting abundance on a global scale.

We can speculate that factors such as habitat and predation pressure on nesting beaches, during oceanic dispersal or where juveniles ultimately disperse to, are important in ultimate nesting success. Many of the high-biomass oceanic habitats favourable for juvenile turtles are also likely to be favoured by their predators, not simulated here. In the North Atlantic, hatchling and juvenile loggerheads use floating *Sargassum* mats as refuge from predation; this protective mechanism may result in greater survivorship for hatchlings, e.g. from the Florida nesting site. An additional potential factor is an oceanic distance from the nesting site at the end of the juvenile period, i.e. how easily an individual can return to the nesting beach using ocean currents [90–92]. Loggerhead females have high nesting fidelity to their natal beaches [20]; we may assume that, if there is a lower energetic swimming cost, nesting females are more likely to successfully return to their natal beach. Moreover, nest counts do not entirely correspond to population abundance because some females may lay multiple clutches in a year and not all females in the population nest each year. Clutch frequency and remigration interval are likely to be related to foraging conditions for adult females, and changes through time can produce wide differences in estimated population sizes [93]. For instance, in some loggerhead populations individuals may nest eight times in a year [94]. How biogeographic variation in these two aspects of sea turtle physiology contributes to differences in nest counts across widely separated areas is not known, but may be a large confounding factor in attempting to relate relative population abundance in loggerhead turtles to hatchling dispersal at a global scale [95].

Nonetheless, at both regional and global scales, some sites are better than others for setting up juveniles for success after the first year and ultimately supporting return of nesting females to the nesting site. For the boundary current associated sites, ultimate dispersal fate varies greatly. For example, while temperatures, dispersal distance and food availability are similar for the Florida and Japan nesting sites (table 2 and figure 3), habitat availability at the end of the first year is divergent. Loggerheads dispersing from Florida are transported to the Azores archipelago [96], which is well known to be a favourable habitat for juvenile turtles [14]. These hatchlings have a suite of behavioural adaptations to make efficient use of the Gulf Stream System with abundant food and *Sargassum* habitat along the way, ultimately arriving at excellent island habitat at the end of the first year [4]. By contrast, loggerhead hatchlings from Japan are transported to the central North Pacific, with the closest coastal foraging habitat still thousands of kilometres away in all directions. These differences in habitat at the end of the first year likely contribute to the ultimate success of hatchlings from the US East Coast in general, and the large number of nests there relative to other boundary current sites [6,35]. There is also a large difference in the oceanographic distance back to the nesting sites for mature turtles between the North Atlantic and North Pacific first-year dispersal fate. Transit times around the North Atlantic gyre are only a few years [15,97]. Transit times across the North Pacific are longer [27], and the energetic costs to return to the nesting site are likely to be much higher.

In contrast with other boundary current sites, mean dispersal distance from Oman is low (810 km; table 2 and figure 4); here no juveniles disperse far from their natal site, spending their first year in a region with persistently warm, productive ocean conditions. It is possible that these favourable conditions lead to higher survivability not only in the first but also in subsequent years when juveniles are more able to control their dispersal through swimming. The added benefit of low dispersal and high food availability is that loggerheads can spend their entire lives close to their natal sites, likely contributing to the high nest abundance in this subpopulation [6,35]. Similarly, hatchlings from the Cape Verde site encounter very high food levels near their nesting site, which along with low dispersal leads to cumulative bioC levels significantly higher than for Florida hatchlings, and similar to hatchlings from Brazil and Japan (figure 4*a*). Despite their transport into the less productive subtropical gyre towards the end of the first year, these hatchlings could be aided in later stages by encountering *Sargassum* habitat not resolved in this simulation [79].

4. Conclusion and future outlook

We have found that the largest rookeries in each subpopulation fall into two classes: those that are closest to major boundary currents that allow easy dispersal to high-biomass regions, and lower dispersal sites in exceptionally productive tropical biomes. In both cases, nesting sites are optimized for easy transport to the most productive open ocean habitat within loggerhead hatchlings' thermal range. Hatchlings with higher potential fitness, determined by their exposure to a simulated food biomass proxy, were associated with colder, more productive waters. Many boundary current associated nesting sites require long transit of hatchlings through narrow coastal migratory corridors with a high likelihood of anthropogenic impacts. Dispersal distance during the first year varied greatly between nesting sites, as did the oceanographic distance from both suitable pre-maturity foraging habitat and nesting beaches at the end of the first year.

The results here are derived from global ocean models, and as such need to be further validated to be applied for loggerhead conservation. This study points the way forward for both observational and directed regional modelling studies to further hone our understanding of what determines favourable pelagic habitat and which hatchlings are the most likely to survive. For example, comparative fitness studies of juvenile turtles in subtropical–subpolar gyre boundaries with juveniles in warmer waters, along with simultaneous forage abundance estimates in each biome, would help constrain the relative effects of forage availability and temperature-dependent growth rates.

While simulated dispersal studies are excellent tools for developing hypotheses, there is much work to be done. This ocean model simulation does not have extreme weather events, which are known to impact turtle dispersal and strandings [98,99]. Ocean models with better near-shore resolution are needed to constrain the early days of the first year, in particular the relative potential for stranding and success of frenzy swimming among the nesting sites. Additionally, ocean models poorly constrain zooplankton food sources for higher trophic level studies, especially biogeochemistry components of Earth system models which are largely designed to study the carbon cycle. In particular, more effort is needed to represent zooplankton functional groups, and in particular gelatinous zooplankton for sea turtle life-history simulations. Finally, the relative impact of passive versus active dispersal on fitness, along with temperature-dependent growth, needs to be determined with a realistic bioenergetic model.

Data accessibility. The Community Earth System Model is freely available at https://www.cesm.ucar.edu. Simulated turtle tracks, including along-track temperature and food data, and sample plotting scripts are available on Open Science Framework (OSF) at doi:10.17605/OSF.IO/YJWK8.

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References

1. Hamann M *et al.* 2010 Global research priorities for sea turtles: informing management and conservation in the 21st century. *Endanger. Species Res.* **11**, 245–269. (doi:10.3354/esr00279)
2. Lutcavage ME, Plotkin P, Witherington B, Lutz PL. 1997 Human impacts on sea turtle survival. In *The biology of sea turtles* (eds PL Lutz, JA Musick), p. 45. London, UK: CRC Press.
3. Hawkes LA, Broderick AC, Godfrey MH, Godley BJ. 2009 Climate change and marine turtles. *Endanger. Species Res.* **7**, 137–154. (doi:10.3354/esr00198)
4. Mansfield KL, Putman NF. 2013 Oceanic habits and habitats. *Biol. Sea Turt.* **3**, 189–211.
5. Mazaris AD, Schofield G, Gkazinou C, Almpanidou V, Hays GC. 2017 Global sea turtle conservation successes. *Sci. Adv.* **3**, e1600730. (doi:10.1126/sciadv.1600730)
6. Casale P, Tucker AD. 2017 *Caretta caretta*. The IUCN Red List of Threatened Species. See https://dx.doi.org/10.2305/IUCN.UK.2017-2.RLTS.T3897A119333622.en.
7. Hawkes LA, Broderick AC, Godfrey MH, Godley BJ. 2007 Investigating the potential impacts of climate change on a marine turtle population. *Glob. Change Biol.* **13**, 923–932. (doi:10.1111/j.1365-2486.2007.01320.x)
8. Fuentes MMPB, Pike DA, Dimatteo A, Wallace BP. 2013 Resilience of marine turtle regional management units to climate change. *Glob. Change Biol.* **19**, 1399–1406. (doi:10.1111/gcb.12138)
9. Anderson JJ, Gurarie E, Bracis C, Burke BJ, Laidre KL. 2013 Modeling climate change impacts on phenology and population dynamics of migratory marine species. *Ecol. Model. Glob. Clim. Change Mar. Ecosyst.* **264**, 83–97. (doi:10.1016/j.ecolmodel.2013.03.009)
10. Rees AF *et al.* 2016 Are we working towards global research priorities for management and conservation of sea turtles? *Endanger. Species Res.* **31**, 337–382. (doi:10.3354/esr00801)
11. Putman NF, Bane JM, Lohmann KJ. 2010 Sea turtle nesting distributions and oceanographic constraints on hatchling migration. *Proc. R. Soc. B* **277**, 3631–3637. (doi:10.1098/rspb.2010.1088)
12. Shillinger GL, Lorenzo ED, Luo H, Bograd SJ, Hazen EL, Bailey H, Spotila JR. 2012 On the dispersal of leatherback turtle hatchlings from Mesoamerican nesting beaches. *Proc. R. Soc. B* **279**, 2391–2395. (doi:10.1098/rspb.2011.2348)
13. Ascani F, Houtan KSV, Lorenzo ED, Polovina JJ, Jones TT. 2016 Juvenile recruitment in loggerhead sea turtles linked to decadal changes in ocean circulation. *Glob. Change Biol.* **22**, 3529–3538. (doi:10.1111/gcb.13331)
14. Carr A. 1987 New perspectives on the pelagic stage of sea turtle development. *Conserv. Biol.* **1**, 103–121. (doi:10.1111/j.1523-1739.1987.tb00020.x)
15. Carr A. 1986 Rips, FADS, and little loggerheads. *BioScience* **36**, 92–100. (doi:10.2307/1310109)
16. Mansfield KL, Wyneken J, Rittschof D, Walsh M, Lim CW, Richards PM. 2012 Satellite tag attachment methods for tracking neonate sea turtles. *Mar. Ecol. Prog. Ser.* **457**, 181–192. (doi:10.3354/meps09485)
17. Mansfield KL, Wyneken J, Porter WP, Luo J. 2014 First satellite tracks of neonate sea turtles redefine the 'lost years' oceanic niche. *Proc. R. Soc. B* **281**, 20133039. (doi:10.1098/rspb.2013.3039)
18. Briscoe DK *et al.* 2016 Multi-year tracking reveals extensive pelagic phase of juvenile loggerhead sea turtles in the North Pacific. *Mov. Ecol.* **4**, 23. (doi:10.1186/s40462-016-0087-4)
19. Shillinger GL, Bailey H, Bograd SJ, Hazen EL, Hamann M, Gaspar P, Godley BJ, Wilson RP, Spotila JR. 2012 Tagging through the stages: technical and ecological challenges in observing life histories through biologging. *Mar. Ecol. Prog. Ser.* **457**, 165–170. (doi:10.3354/meps09816)
20. Bolten AB, Bjorndal KA, Martins HR, Dellinger T, Biscoito MJ, Encalada SE, Bowen BW. 1998 Transatlantic developmental migrations of loggerhead sea turtles demonstrated by mtDNA sequence analysis. *Ecol. Appl.* **8**, 1–7. (doi:10.1890/1051-0761(1998)008[0001:TDMOLS]2.0.CO;2)
21. 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. (doi:10.1098/rspb.2008.1931)
22. Putman NF, Verley P, Shay TJ, Lohmann KJ. 2012 Simulating transoceanic migrations of young loggerhead sea turtles: merging magnetic navigation behavior with an ocean circulation model. *J. Exp. Biol.* **215**, 1863–1870. (doi:10.1242/jeb.067587)
23. Scott R, Marsh R, Hays GC. 2012 A little movement orientated to the geomagnetic field makes a big difference in strong flows. *Mar. Biol.* **159**, 481–488. (doi:10.1007/s00227-011-1825-1)
24. Gaspar P, Benson SR, Dutton PH, Réveillère A, Jacob G, Meetoo C, Dehecq A, Fossette S. 2012 Oceanic dispersal of juvenile leatherback turtles: going beyond passive drift modeling. *Mar. Ecol. Prog. Ser.* **457**, 265–284. (doi:10.3354/meps09689)
25. Abecassis M, Senina I, Lehodey P, Gaspar P, Parker D, Balazs G, Polovina J. 2013 A model of loggerhead sea turtle (*Caretta caretta*) habitat and movement in the oceanic North Pacific. *PLoS ONE* **8**, e73274. (doi:10.1371/journal.pone.0073274)
26. Robson NA, Hetzel Y, Whiting S, Wijeratne S, Pattiaratchi CB, Withers P, Thums M. 2017 Use of particle tracking to determine optimal release dates and locations for rehabilitated neonate sea turtles. *Front. Mar. Sci.* **4**, 173. (doi:10.3389/fmars.2017.00173)
27. Okuyama J, Kitagawa T, Zenimoto K, Kimura S, Arai N, Sasai Y, Sasaki H. 2011 Trans-Pacific dispersal of loggerhead turtle hatchlings inferred from numerical simulation modeling. *Mar. Biol.* **158**, 2055–2063. (doi:10.1007/s00227-011-1712-9)
28. Lalire M, Gaspar P. 2019 Modeling the active dispersal of juvenile leatherback turtles in the North Atlantic Ocean. *Mov. Ecol.* **7**, 7. (doi:10.1186/s40462-019-0149-5)
29. Harrison CS, Siegel DA, Mitarai S. 2013 Filamentation and eddy-eddy interactions in marine larval accumulation and transport. *Mar. Ecol. Prog. Ser.* **472**, 27–44. (doi:10.3354/meps10061)
30. Putman NF, He R. 2013 Tracking the long-distance dispersal of marine organisms: sensitivity to ocean model resolution. *J. R. Soc. Interface* **10**, 20120979. (doi:10.1098/rsif.2012.0979)
31. Clayton S, Dutkiewicz S, Jahn O, Hill C, Heimbach P, Follows MJ. 2017 Biogeochemical versus ecological consequences of modeled ocean physics. *Biogeosci. Katlenburg-Lindau* **14**, 2877–2889. (doi:10.5194/bg-14-2877-2017)
32. Rohr T, Long MC, Kavanaugh MT, Lindsay K, Doney SC. 2017 Variability in the mechanisms controlling Southern Ocean phytoplankton bloom phenology in an ocean model and satellite observations. *Global Biogeochem. Cycles* **31**, 922–940. (doi:10.1002/2016GB005615)
33. Harrison CS, Long MC, Lovenduski NS, Moore JK. 2018 Mesoscale effects on carbon export: a global perspective. *Global Biogeochem. Cycles* **32**, 680–703. (doi:10.1002/2017GB005751)
34. Petrik CM, Stock CA, Andersen KH, van Denderen PD, Watson JR. 2019 Bottom-up drivers of global patterns of demersal, forage, and pelagic fishes. *Prog. Oceanogr.* **176**, 102124. (doi:10.1016/j.pocean.2019.102124)
35. Bowen BW, Kamezaki N, Limpus CJ, Hughes GR, Meylan AB, Avise JC. 1994 Global phylogeography of the loggerhead turtle (*Caretta caretta*) as indicated by mitochondrial DNA haplotypes. *Evolution* **48**, 1820–1828. (doi:10.2307/2410511)
36. Wallace BP *et al.* 2010 Regional management units for marine turtles: a novel framework for prioritizing conservation and research across multiple scales. *PLoS ONE* **5**, e15465. (doi:10.1371/journal.pone.0015465)
37. Wyneken J, Salmon M. 1992 Frenzy and post-frenzy swimming activity in loggerhead, green, and leatherback hatchling sea turtles. *Copeia* **1992**, 478–484. (doi:10.2307/1446208)

38. Putman NF, Verley P, Endres CS, Lohmann KJ. 2015 Magnetic navigation behavior and the oceanic ecology of young loggerhead sea turtles. *J. Exp. Biol.* **218**, 1044–1050. (doi:10.1242/jeb.109975)
39. Putman NF *et al.* 2014 Numerical dispersal simulations and genetics help explain the origin of hawksbill sea turtles in Ascension Island. *J. Exp. Mar. Biol. Ecol.* **450**, 98–108. (doi:10.1016/j.jembe.2013.10.026)
40. Putman NF, Scott R, Verley P, Marsh R, Hays GC. 2012 Natal site and offshore swimming influence fitness and long-distance ocean transport in young sea turtles. *Mar. Biol.* **159**, 2117–2126. (doi:10.1007/s00227-012-1995-5)
41. Putman NF, Naro-Maciel E. 2013 Finding the 'lost years' in green turtles: insights from ocean circulation models and genetic analysis. *Proc. R. Soc. B* **280**, 20131468. (doi:10.1098/rspb.2013.1468)
42. Putman NF, Lohmann KJ, Putman EM, Quinn TP, Klimley AP, Noakes DLG. 2013 Evidence for geomagnetic imprinting as a homing mechanism in Pacific Salmon. *Curr. Biol.* **23**, 312–316. (doi:10.1016/j.cub.2012.12.041)
43. Putman NF *et al.* 2020 Predicted distributions and abundances of the sea turtle 'lost years' in the western North Atlantic Ocean. *Ecography* **43**, 506–517. (doi:10.1111/ecog.04929)
44. Large WG, Yeager SG. 2004 Diurnal to decadal global forcing for ocean and sea-ice models: the data sets and flux climatologies. No. NCAR/TN-460+STR. University Corporation for Atmospheric Research. See https://doi.org/10.5065/D6KK98Q6.
45. Laufkötter C *et al.* 2016 Projected decreases in future marine export production: the role of the carbon flux through the upper ocean ecosystem. *Biogeosciences* **13**, 19 941–19 998. (doi:10.5194/bg-13-4023-2016)
46. Moore JK, Doney SC, Lindsay K. 2004 Upper ocean ecosystem dynamics and iron cycling in a global three-dimensional model. *Global Biogeochem. Cycles* **18**, GB4028. (doi:10.1029/2004GB002220)
47. Rohr T, Harrison C, Long MC, Gaube P, Doney SC. 2020 Eddy-modified iron, light, and phytoplankton cell division rates in the simulated Southern Ocean. *Global Biogeochem. Cycles* **34**, e2019GB006380. (doi:10.1029/2019GB006380)
48. Paris CB, Helgers J, van Sebille E, Srinivasan A. 2013 Connectivity modeling system: a probabilistic modeling tool for the multi-scale tracking of biotic and abiotic variability in the ocean. *Environ. Model. Softw.* **42**, 47–54. (doi:10.1016/j.envsoft.2012.12.006)
49. Kough AS, Paris CB, Iv MJB. 2013 Larval connectivity and the international management of fisheries. *PLoS ONE* **8**, e64970. (doi:10.1371/journal.pone.0064970)
50. Rossi V, Van Sebille E, Sen Gupta A, Garçon V, England MH. 2013 Multi-decadal projections of surface and interior pathways of the Fukushima cesium-137 radioactive plume. *Deep Sea Res. Part Oceanogr. Res. Pap.* **80**, 37–46. (doi:10.1016/j.dsr.2013.05.015)
51. Wood S, Paris CB, Ridgwell A, Hendy EJ. 2014 Modelling dispersal and connectivity of broadcast spawning corals at the global scale. *Glob. Ecol. Biogeogr.* **23**, 1–11. (doi:10.1111/geb.12101)
52. Epperly SP, Braun J, Chester AJ, Cross FA, Merriner JV, Tester PA. 1995 Winter distribution of sea turtles in the vicinity of Cape Hatteras and their interactions with the summer flounder trawl fishery. *Bull. Mar. Sci.* **56**, 547–568.
53. Coles WC, Musick JA. 2000 Satellite sea surface temperature analysis and correlation with sea turtle distribution off North Carolina. *Copeia* **2000**, 551–554. (doi:10.1643/0045-8511(2000)000[0551:SSSTAA]2.0.CO;2)
54. Polovina JJ, Balazs GH, Howell EA, Parker DM, Seki MP, Dutton PH. 2004 Forage and migration habitat of loggerhead (*Caretta caretta*) and olive ridley (*Lepidochelys olivacea*) sea turtles in the central North Pacific Ocean. *Fish. Oceanogr.* **13**, 36–51. (doi:10.1046/j.1365-2419.2003.00270.x)
55. Schwartz FJ. 1978 Behavioral and tolerance responses to cold water temperatures by three species of sea turtles (Reptilia, Cheloniidae) in North Carolina. *Fla. Mar. Res. Publ. No.* **33**, 16–18.
56. Davenport J. 1997 Temperature and the life-history strategies of sea turtles. *J. Therm. Biol.* **22**, 479–488. (doi:10.1016/S0306-4565(97)00066-1)
57. Young JW *et al.* 2015 The trophodynamics of marine top predators: current knowledge, recent advances and challenges. *Deep Sea Res. Part II Top. Stud. Oceanogr.* **113**, 170–187. (doi:10.1016/j.dsr2.2014.05.015)
58. Stock CA *et al.* 2011 On the use of IPCC-class models to assess the impact of climate on living marine resources. *Prog. Oceanogr.* **88**, 1–27. (doi:10.1016/j.pocean.2010.09.001)
59. Westberry T, Behrenfeld MJ, Siegel DA, Boss E. 2008 Carbon-based primary productivity modeling with vertically resolved photoacclimation. *Global Biogeochem. Cycles* **22**, GB2024. (doi:10.1029/2007GB003078)
60. Friedland KD, Stock C, Drinkwater KF, Link JS, Leaf RT, Shank BV, Rose JM, Pilskaln CH, Fogarty MJ. 2012 Pathways between primary production and fisheries yields of large marine ecosystems. *PLoS ONE* **7**, e28945. (doi:10.1371/journal.pone.0028945)
61. Moriarty R, O'Brien TD. 2013 Distribution of mesozooplankton biomass in the global ocean. *Earth Syst. Sci. Data* **5**, 45–55. (doi:10.5194/essd-5-45-2013)
62. Luo JY, Condon RH, Stock CA, Duarte CM, Lucas CH, Pitt KA, Cowen RK. 2020 Gelatinous zooplankton-mediated carbon flows in the global oceans: a data-driven modeling study. *Global Biogeochem. Cycles* **34**, e2020GB006704. (doi:10.1029/2020GB006704)
63. Stock CA, Dunne JP, John JG. 2014 Global-scale carbon and energy flows through the marine planktonic food web: an analysis with a coupled physical–biological model. *Prog. Oceanogr.* **120**, 1–28. (doi:10.1016/j.pocean.2013.07.001)
64. Chassignet EP, Marshall J. 2008 Gulf Stream separation in numerical ocean models. In *Ocean modeling in an eddying regime, geophysical monograph series* (eds MW Hecht, H Hasumi), pp. 39–61. Washington, DC: American Geophysical Union.
65. Ezer T. 2016 Revisiting the problem of the Gulf Stream separation: on the representation of topography in ocean models with different types of vertical grids. *Ocean Model* **104**, 15–27. (doi:10.1016/j.ocemod.2016.05.008)
66. Capet XJ, Marchesiello P, McWilliams JC. 2004 Upwelling response to coastal wind profiles. *Geophys. Res. Lett.* **31**, L13311. (doi:10.1029/2004GL020123)
67. Small RJ, Curchitser E, Hedstrom K, Kauffman B, Large WG. 2015 The Benguela upwelling system: quantifying the sensitivity to resolution and coastal wind representation in a global climate model. *J. Clim.* **28**, 9409–9432. (doi:10.1175/JCLI-D-15-0192.1)
68. Bopp L *et al.* 2013 Multiple stressors of ocean ecosystems in the 21st century: projections with CMIP5 models. *Biogeosciences* **10**, 6225–6245. (doi:10.5194/bg-10-6225-2013)
69. Putman N. 2018 Marine migrations. *Curr. Biol.* **28**, R972–R976. (doi:10.1016/j.cub.2018.07.036)
70. Dodd Jr CK. 1988 Synopsis of the biological data on the loggerhead sea turtle Caretta caretta (Linnaeus 1758). US Fish Wildl. Serv. *Biol. Rep.* **88**. See http://www.fao.org/3/ap959e/ap959e.pdf.
71. Smith RL, Huyer A, Godfrey JS, Church JA. 1991 The Leeuwin Current off Western Australia, 1986–1987. *J. Phys. Oceanogr.* **21**, 323–345. (doi:10.1175/1520-0485(1991)021<0323:TLCOWA>2.0.CO;2)
72. Jickells TD *et al.* 2005 Global iron connections between desert dust, ocean biogeochemistry, and climate. *Science* **308**, 67–71. (doi:10.1126/science.1105959)
73. Guieu C, Al Azhar M, Aumont O, Mahowald N, Levy M, Ethé C, Lachkar Z. 2019 Major impact of dust deposition on the productivity of the Arabian Sea. *Geophys. Res. Lett.* **46**, 6736–6744. (doi:10.1029/2019GL082770)
74. Currie RI, Fisher AE, Hargreaves PM. 1973 Arabian Sea upwelling. In *The biology of the Indian Ocean, ecological studies* (eds B Zeitzschel, SA Gerlach), pp. 37–52. Berlin, Germany: Springer.
75. Yi X, Hünicke B, Tim N, Zorita E. 2018 The relationship between Arabian Sea upwelling and Indian Monsoon revisited in a high resolution ocean simulation. *Clim. Dyn.* **50**, 201–213. (doi:10.1007/s00382-017-3599-8)
76. Maxwell SM *et al.* 2015 Dynamic ocean management: defining and conceptualizing real-time management of the ocean. *Mar. Policy* **58**, 42–50. (doi:10.1016/j.marpol.2015.03.014)
77. Howell E, Kobayashi D, Parker D, Balazs G, Polovina AJJ. 2008 TurtleWatch: a tool to aid in the bycatch reduction of loggerhead turtles *Caretta caretta* in the Hawaii-based pelagic longline fishery. *Endanger. Species Res.* **5**, 267–278. (doi:10.3354/esr00096)
78. NOAA Fisheries. 2019 Loggerhead turtle—Northwest Atlantic Ocean DPS critical habitat map. See https://www.fisheries.noaa.gov/resource/map/loggerhead-turtle-northwest-atlantic-ocean-dps-critical-habitat-map (accessed 7 January 2019).

79. Brooks MT, Coles VJ, Hood RR, Gower JFR. 2018 Factors controlling the seasonal distribution of pelagic *Sargassum*. *Mar. Ecol. Prog. Ser.* **599**, 1–18. (doi:10.3354/meps12646)
80. Mansfield KL, Saba VS, Keinath JA, Musick JA. 2009 Satellite tracking reveals a dichotomy in migration strategies among juvenile loggerhead turtles in the Northwest Atlantic. *Mar. Biol.* **156**, 2555. (doi:10.1007/s00227-009-1279-x)
81. Lewison R, Wallace B, Alfaro-Shigueto J, Mangel J, Maxwell S, Hazen E. 2013 Fisheries bycatch of marine turtles: lessons learned from decades of research and conservation. In *The biology of sea turtles,* vol. III, pp. 329–352. Boca Raton, FL: CRC Press.
82. Schuyler QA, Wilcox C, Townsend KA, Wedemeyer-Strombel KR, Balazs G, Sebille E, Hardesty BD. 2016 Risk analysis reveals global hotspots for marine debris ingestion by sea turtles. *Glob. Change Biol.* **22**, 567–576. (doi:10.1111/gcb.13078)
83. Salmon M, Wyneken J. 1987 Orientation and swimming behavior of hatchling loggerhead turtles *Caretta caretta* L. during their offshore migration. *J. Exp. Mar. Bioi. Ecol.* **109**, 137–153. (doi:10.1016/0022-0981(87)90012-8)
84. 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. (doi:10.1007/s00227-008-1074-0)
85. Lohmann KJ, Putman NF, Lohmann CM. 2012 The magnetic map of hatchling loggerhead sea turtles. *Curr. Opin. Neurobiol. Neuroethol.* **22**, 336–342. (doi:10.1016/j.conb.2011.11.005)
86. Mansfield KL, Mendilaharsu ML, Putman NF, Marcovaldi MAG, Sacco AE, Lopez G, Pires T, Swimmer Y. 2017 First satellite tracks of South Atlantic sea turtle 'lost years': seasonal variation in trans-equatorial movement. *Proc. R. Soc. B* **284**, 20171730. (doi:10.1098/rspb.2017.1730)
87. Putman NF, Mansfield KL. 2015 Direct evidence of swimming demonstrates active dispersal in the sea turtle 'lost years.' *Curr. Biol.* **25**, 1221–1227. (doi:10.1016/j.cub.2015.03.014)
88. Pike DA. 2013 Climate influences the global distribution of sea turtle nesting. *Glob. Ecol. Biogeogr.* **22**, 555–566. (doi:10.1111/geb.12025)
89. Kot CY, Fujioka E, DiMatteo AD, Wallace BP, Hutchinson BJ, Cleary J, Halpin PN, Mast RB. 2021 The state of the world's sea turtles online database: data provided by the SWOT Team and hosted on OBIS-SEAMAP. Oceanic Society, Conservation International, IUCN Marine Turtle Specialist Group (MTSG) and Marine Geospatial Ecology Lab, Duke University. See http://seamap.env.duke.edu/swot. (accessed 8 January 2019).
90. Watson JR, Hays CG, Raimondi PT, Mitarai S, Dong C, McWilliams JC, Blanchette CA, Caselle JE, Siegel DA. 2011 Currents connecting communities: nearshore community similarity and ocean circulation. *Ecology* **92**, 1193–1200. (doi:10.1890/10-1436.1)
91. Hays GC, Scott R. 2013 Global patterns for upper ceilings on migration distance in sea turtles and comparisons with fish, birds and mammals. *Funct. Ecol.* **27**, 748–756. (doi:10.1111/1365-2435.12073)
92. Jönsson BF, Watson JR. 2016 The timescales of global surface-ocean connectivity. *Nat. Commun.* **7**, 11239. (doi:10.1038/ncomms11239)
93. Esteban N, Mortime JA, Hays GC. 2017 How numbers of nesting sea turtles can be overestimated by nearly a factor of two. *Proc. R. Soc. B* **284**, 20162581. (doi:10.1098/rspb.2016.2581)
94. Tucker AD. 2010 Nest site fidelity and clutch frequency of loggerhead turtles are better elucidated by satellite telemetry than by nocturnal tagging efforts: implications for stock estimation. *J. Exp. Mar. Biol. Ecol.* **383**, 48–55. (doi:10.1016/j.jembe.2009.11.009)
95. Hays GC. 2000 The implications of variable remigration intervals for the assessment of population size in marine turtles. *J. Theor. Biol.* **206**, 221–227. (doi:10.1006/jtbi.2000.2116)
96. Sala I, Harrison CS, Caldeira RMA. 2016 The role of the Azores archipelago in capturing and retaining incoming particles. *J. Mar. Syst.* **154**, 146–156. (doi:10.1016/j.jmarsys.2015.10.001)
97. Hays GC, Marsh R. 1997 Estimating the age of juvenile loggerhead sea turtles in the North Atlantic. *Can. J. Zool.* **75**, 40–46. (doi:10.1139/z97-005)
98. Monzón-Argüello C *et al.* 2012 Lost at sea: genetic, oceanographic and meteorological evidence for storm-forced dispersal. *J. R. Soc. Interface* **9**, 1725–1732. (doi:10.1098/rsif.2011.0788)
99. DuBois MJ, Putman NF, Piacenza SE. 2020 Hurricane frequency and intensity may decrease dispersal of Kemp's ridley sea turtle hatchlings in the Gulf of Mexico. *Front. Mar. Sci.* **7**, 301. (doi:10.3389/fmars.2020.00301)
100. Thyng K, Greene C, Hetland R, Zimmerle H, DiMarco S. 2016 True colors of oceanography: guidelines for effective and accurate colormap selection. *Oceanography* **29**, 9–13. (doi:10.5670/oceanog.2016.66)