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# Nano-tags for neonates and ocean-mediated swimming behaviours linked to rapid dispersal of hatchling sea turtles

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Dispersal during juvenile life stages drives the life-history evolution and dynamics of many marine vertebrate populations. However, the movements of juvenile organisms, too small to track using conventional satellite telemetry devices, remain enigmatic. For sea turtles, this led to the paradigm of the 'lost years' since hatchlings disperse widely with ocean currents. Recently, advances in the miniaturization of tracking technology have permitted the application of nano-tags to track cryptic organisms. Here, the novel use of acoustic nano-tags on neonate loggerhead turtle hatchlings enabled us to witness first-hand their dispersal and behaviour during their first day at sea. We tracked hatchlings distances of up to 15 km and documented their rapid transport (up to $60\,\mathrm{m\,min^{-1}}$) with surface current flows passing their natal areas. Tracking was complemented with laboratory observations to monitor swimming behaviours over longer periods which highlighted (i) a positive correlation between swimming activity levels and body size and (ii) population-specific swimming behaviours (e.g. nocturnal inactivity) suggesting local oceanic conditions drive the evolution of innate swimming behaviours. Knowledge of the swimming behaviours of small organisms is crucial to improve the accuracy of ocean model simulations used to predict the fate of these organisms and determine resultant population-level implications into adulthood.

## 1. Introduction

The high mobility of many organisms presents a variety of research and conservation management challenges [1]. In the marine realm, the movements of some fish, mammals and sea turtles can span 1000s of kilometres between their breeding and feeding habitats. The journeys of adult sea turtles, whales and sharks are now routinely documented with the use of satellite tags [2] which provide near real-time location uplinks of organisms through the ARGOS satellite array. This technology has provided crucial insights into animal life histories and the extent of their home-ranges which can span the jurisdictions of multiple nations and hence encompass a diversity of habitats and associated threats [2]. Consequently, tracking datasets are now proving to have great conservation utility with regards to informing spatially and temporally relevant conservation legislation such as Marine Protected Areas [3–5]. However, much remains to be discovered about species and early life stages which are too small to be tracked via satellite, yet can also disperse several 1000s of kilometres with ocean current flows from their natal areas to development habitats/settlement sites [6,7]. With recent advances in the resolution of ocean models [8], computer model simulations of current flows are gaining application to predict the dispersal pathways of small organisms like hatchling sea turtles and fish larvae [6,7,9–12].

Hatchling sea turtles perform some of the longest journeys in the animal kingdom while dispersing with surface ocean currents from their natal areas to juvenile development habitats [13]. However, this early life phase is still commonly referred to as the 'lost years' (after Carr [14]) as hatchlings effectively disappear in the sea after emerging from their nests. The use of oceanographic approaches to model the cryptic dispersal pathways of small organisms during the 'lost' period has led to key discoveries, for example, into the population dynamics, breeding strategies (reproductive age/philopatric behaviours) and the ontogeny of subsequent active long-distance migrations for endangered species like turtles [6,7,11,15]. For instance by combining satellite tracking with oceanographic tools to study the global movement patterns of adult and neonate hatchling sea turtles (respectively), a conceptual advance in movement ecology emerged; passive drift experiences of hatchlings drive the subsequent ontogeny of their regular active adult breeding migrations [11]. While adult turtles are strong swimmers that travel counter to prevailing current flows (between natal breeding and foraging habitats), the diversity in global migration patterns/foraging strategies were consistently linked to the fate of dispersing hatchlings [11]. Studying the dispersal of small organisms is thus of particular importance as early life stages have important consequences that can drive the ontogeny of behaviours throughout adulthood.

Despite the increasing use and accepted utility of ocean models to study prevailing dispersal pathways, even the smallest organisms are not entirely passive. There is thus an urgent need for accurate data on the behaviour of hatchlings and other drifting organisms to optimize the realism of drift simulations. For example, the ability of small organisms to alter their dispersal outcomes through directional horizontal swimming is now becoming apparent [10,16,17] as small organisms (e.g. sea turtles and larval fish) can attain relatively high swimming speeds [18,19] and may elicit oriented swimming responses to a range of environmental cues [16,20,21]. Hatchling sea turtles can be considered among the most active drifters as when they enter the sea they embark on an initial 'swimming frenzy' (a period of hyperactive offshore swimming) which lasts several days. This frenzy period helps hatchlings to escape predator-rich coastal waters and reach the offshore surface ocean currents [10]; the primary determinant of their subsequent dispersal [12]. As hatchlings are too small for conventional satellite tracking technology, knowledge of the 'swimming frenzy' remains reliant on direct observational/experimental approaches and has been best described from laboratory studies on loggerhead turtles (*Caretta caretta*) in the southeastern USA (e.g. [22]).

Emerging laboratory studies are starting to reveal significant differences in the innate swimming behaviours of hatchling sea turtles; with intra-species population variation thought to arise from local oceanic conditions present at the respective natal areas [22,23]. Attempts to gain natural field data on the offshore swimming behaviours of neonate hatchlings have been limited in quantity and scope due to the reliance on direct observations and the use of snorkelers/boats to follow hatchlings at sea [24–30]. During these efforts, floats (up to 10 cm long and 5 g) are typically equipped on hatchlings to help keep hatchlings within visual contact or to carry 1.1–4.9 g radio/acoustic tags. Recent miniaturization of acoustic tagging technology has led to small (0.65 g) and streamlined devices which can be directly equipped on hatchling sea turtles to minimize drag impacts [31].

In order to gain insights into the evolution of the swimming behaviours of neonate loggerhead turtles, here we combined (i) well-established experimental laboratory techniques, e.g. [18,22,23] with (ii) recently trailed at sea acoustic tracking [31] and (iii) high-resolution ocean model data [32]. We focused on the Cape Verde Islands which host the World's third largest [33], and highly philopatric [34] nesting population of loggerhead turtles which are genetically isolated from other Atlantic and Mediterranean rookeries [12]. Owing to the oceanic location of these islands, this nesting aggregation is exposed to very different ocean current regimes than coastal mainland sites where studies into loggerhead turtle hatchling swimming behaviour have focused. These local ocean current regimes that drive hatchling dispersion from this region are believed to have contributed towards the ontogeny of a dichotomy in the post-breeding migration/foraging strategies performed by the adult Cape Verdean turtles [11], with the majority of adults feeding oceanically, while only a minority adopt more typical neritic feeding strategies [35,36]. Furthermore, turtle populations that use foraging habitats in the Eastern Atlantic region face particularly high threats from pelagic fisheries [37], hence there is an urgent need for a greater understanding into the movement behaviours of both juvenile and adult turtles to aid conservation efforts. Consequently, by using recent advancements in the miniaturization of tracking technologies in conjunction with laboratory observations and a high-resolution assimilated ocean model, we assessed the extent to which local oceanic conditions may drive the evolution of innate population-specific swimming behaviours in neonate hatchlings.

## 2. Material and methods

### (a) Hatchling collection

Fieldwork was conducted on the island of Boa Vista, the easternmost Cape Verdean Island (figure 1a) which supports up to 90% of the archipelago's loggerhead turtle nesting activity [33]. Hatchlings were obtained from a hatchery and natural *in situ* nests. The hatchery was located on a beach at the southernmost tip of the island (15°58′17 N, 22°47′56 W) and natural *in situ* nests used were located within *ca* 300 m of the hatchery or from a beach situated in the northwest of the island (16°10′14 N, 22°54′53 W) (figure 1a, inset). See the electronic supplementary material for further information.

### (b) Acoustic tracking

Acoustic tracking of hatchlings was conducted between 26 September and the 17 October 2013 from the two aforementioned nesting beaches located in the south and northwest of the island. Following the methods of Thums *et al.* [31], coded V5 acoustic transmitters operating with a 10 s average ping frequency at 180 kHz (Vemco Ltd, Halifax, Canada) were glued to the plastron of hatchlings using a small drop of a non-toxic adhesive (Vetbond). This adhesive is expected to break down naturally allowing the tags to detach in a few days [38]. On seven occasions, tags were easily removed without any harm to the hatchlings at the end of the tracking period. The V5 tags weigh 0.4 g in water (0.65 g in air) and measure 12 mm long by 5 mm wide, hence their small streamlined shape helps minimize drag impacts [39]. The average mass of tracked hatchlings was 19.46 g (range 17.00–23.00 g). The tags were glued to the plastron of hatchlings 1 h prior to release (figure 1b). Hatchlings were first placed into a container of seawater which confirmed
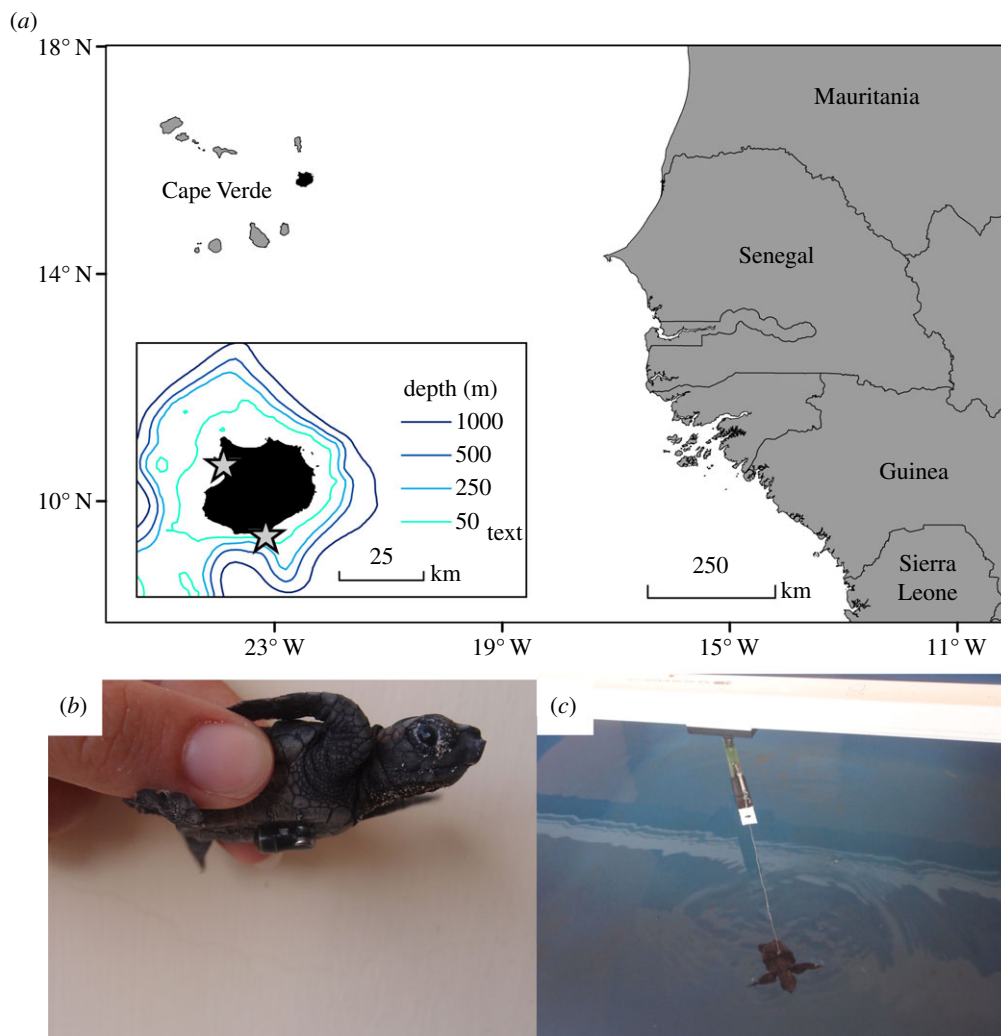
**Figure 1.** (*a*) Location of the Eastern Atlantic Cape Verde Islands, with Boa Vista, the most eastern island, depicted in black (and in the inset). Map inset: stars depict location of nesting beaches from which hatchlings were obtained/tracked. Bathymetry contours (from the Gebco ETOPO1 1 Arc-Minute Global Relief Model) highlight the very narrow continental shelf (depth of approximately less than 250 m) around the east and south of the island. (*b*) A 12 mm long Vemco V-5 acoustic nano-tag glued to the plastron of a hatchling turtle. (*c*) One of two identical indoor swimming arenas used to monitor the daily swimming activity of hatchlings (proportion of time spent swimming). For scale, the rotating horizontal arm is 15 cm in length. (Online version in colour.)

no obvious impacts on swimming behaviour. Tracking was conducted during daylight hours and hatchlings were placed in the sea just past the shore-break and left for 10 min to acclimatize/establish a course. Hatchlings were then followed using a small (*ca* 6 m) boat with a Vemco VR100 mobile acoustic receiver and directional hydrophone which enabled the approximate direction of the turtle to be determined. Where possible, the boat remained within a distance of *ca* 20 m behind the hatchlings at all times and the receiver detected and stored all acoustic tag signals along with the date/time and GPS location of the receiver (see the electronic supplementary material for further information).

## (c) Laboratory observations of the swimming frenzy

Laboratory observations of hatchling swimming behaviour were conducted between the 19 September and 3 November 2013. Two identical adjacent swimming arenas (1 m length × 1 m width × 0.7 m height) were set up and seawater was filled to a depth of 60 cm. Two hatchlings from the same nest were used for each experimental trial with a single hatchling placed in each arena. Each hatchling was fitted with a lycra harness; a *ca* 2 cm wide strip of lycra wrapped around the widest point of the hatchlings carapace. This design avoided the harness coming into contact with any of the flippers/surrounding skin and muscle that could impede swimming. The harness was attached with monofilament

fishing line (22 cm in length) to a switch at the end of a horizontal arm (15 cm in length) positioned above the arena and free to rotate 360° (adapted from [22]). Hatchlings could make shallow dives and the set-up ensured hatchlings were always at least 10 cm from the sides of the arenas. When hatchlings swam using their fore-flippers, tension on the string activated the switch which completed an electric circuit; used to record periods of active swimming. When hatchlings were inactive (i.e. sleeping) or just using their rear flippers to make small surface movements (e.g. while briefly resting/surfacing to breath), the switches were deactivated to record periods of inactivity (figure 1*c*). Hatchlings were monitored in the tanks for 3–7 days and released offshore following the end of each experiment (see the electronic supplementary material for further information).

## 3. Data analysis

### (a) Acoustic tracking

Latitude and longitude coordinates from acoustic tracking data were plotted in ArcGIS software. For each hatchling, travel speeds are calculated based on their cumulative travel distances during each 0.5 km displacement from their starting locations. A mixed effect linear model (LME) was
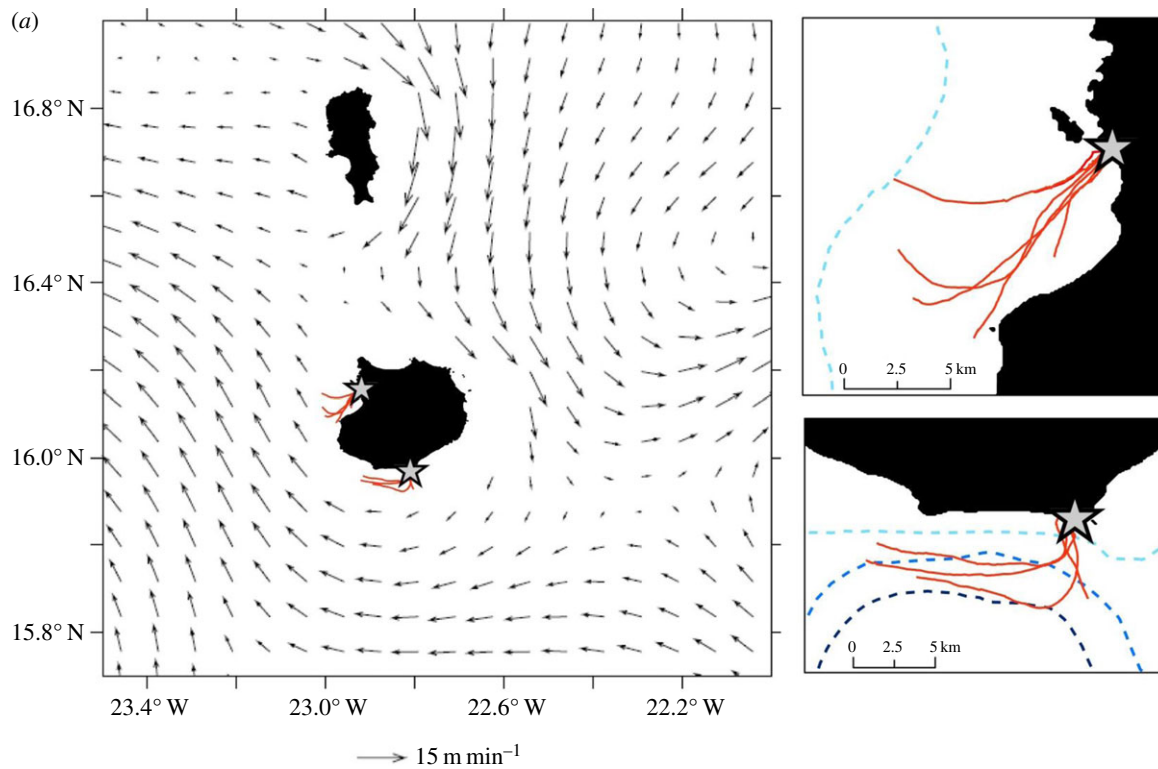
**Figure 2.** (*a*) Trajectories of hatchlings acoustically tracked from two nesting beaches (stars) with mean current flow vectors plotted during the tracking period (26 Sept – 17 Oct). Flow vector length corresponds to current speed. Finer scale insets are also included to provide a more detailed view of the tracks. The 50, 250 and 500 m depth contours are also plotted (light – dark). Top inset: hatchlings maintained fairly consistent headings away from the northwestern beach until reaching distances of *ca* 9 – 12 km when currents flowing broadly NNW started to transport hatchlings offshore in this direction. Bottom inset: hatchlings travelled *ca* 3 – 6 km offshore from the southern beach until currents flowing broadly west transported them along the coast in this direction. (Online version in colour.)

used to assess the impact of beach location and displacement distance on travel speeds with turtle ID included as a random effect. An operational ocean model (http://www.mercator-ocean.fr) was used to obtain ocean current flow data. The global model configuration is based on the NEMO code [40] and assimilates *in situ* ocean and satellite data [32], thus representing a realistic state of the upper ocean current variability. Here, we use daily averages from the 1/12th of a degree version (ORCA12, PSY4V2R2) with a grid resolution of approximately 9 km around the Cape Verde Islands. During tracking periods, local wind data were obtained from forecasts based on the Global Forecast System model with a 27 km horizontal resolution (www.windfinder.com).

## (b) Laboratory observations of the swimming frenzy

In the swimming arena experiments, the proportion of time spent swimming was calculated for (i) each 24 h period (from hereafter referred to as 'days') since the time hatchlings were placed in tanks and (ii) for each nocturnal and diurnal period defined by the corresponding daily time of sunrise and sunset. Proportion data were arcsine transformed and due to the unbalanced nature of our results (arising from a corrupt data file during day 1 of the third experimental trial and different sample sizes associated with different time periods) a LME model was used to assess the significance of explanatory variables on the proportion of time spent swimming. Explanatory variables included arena ID (to test any effect of the two different tanks), body mass of hatchlings and time period. Hatchling ID was included as a random effect in all LME models. An initial LME model with just nest ID as an explanatory variable revealed that the non-independence of data

associated with hatchling relatedness (two hatchlings from each nest were trailed simultaneously) was not significant ($F_{7,8} = 1.3414$, $p = 0.343$) and hence nest ID was not included as a random interaction term. Paired *t*-tests were also conducted to test whether the proportion of time spent active varied between subsequent time periods when data were available for at least 10 of the same individuals.

## 4. Results

### (a) Tracking

A total of 11 hatchlings were tracked; three from *in situ* nests (two from the northwestern nesting beach and one from the southern nesting beach) and eight from the hatchery in the south. The first hatchling was tracked for 20 min, while the rest were all tracked for between 3 to *ca* 8 h. One hatchling is believed to have succumbed to a predatory fish. Hatchlings were tracked on journeys of up to 15 km and attained displacement distances of 12 km from their starting locations (figure 2). During the tracking period (26 September to 17 October), Boa Vista was subject to anticyclonic (clockwise) surface currents, with typical speeds (mean ± s.d.) of $9.3 \pm 2.3$ m min$^{-1}$ (electronic supplementary material, figure S1). In particular, the southern and western regions of the island featured a general westward/northwestward flow, which resembles the long-term flow pattern, although varying in intensity. Sea state ranged from 1 to 5 on the Beaufort scale with highly variable wind speeds (between *ca* 3 and 20 knots) and periods of high swell.

The LME model showed that hatchling travel speeds increased with increasing displacement distances ($F_{25,149} = 5.64$,
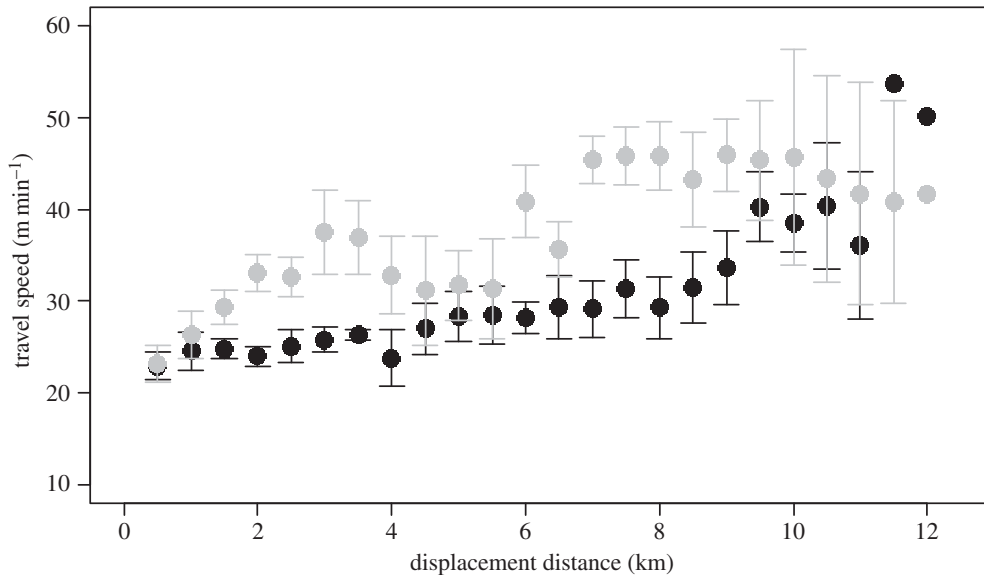
**Figure 3.** Mean swimming speeds (with s.e. bars) are plotted, based on the total cumulative distance hatchlings travelled during each 0.5 km displacement distance from their respective starting locations (grey: southern nesting beach, black: northern nesting beach). Travel speeds were consistently higher and tended to be more variable from the southern nesting beach until displacement distances of around 9–12 km revealing that hatchlings encountered favourable surface current flows quicker in the south.

$p < 0.001$) and tracking location also had a significant effect on travel speeds ($F_{1,9} = 6.26$, $p < 0.05$) with turtles from the south attaining higher speeds than those from the northwest (figure 3). Within the first 0.5 km, hatchlings swam offshore with similar travel speeds observed between the two locations (range: 19–29 m min$^{-1}$ from the northwest and 19–27 m min$^{-1}$ from the south). No significant effects of body size on travel speeds were found. From the south, travel speeds of more than 40 m min$^{-1}$ were attained at displacement distances of 3 km after *ca* 2 h of swimming and speeds of 58 m min$^{-1}$ were attained after *ca* 5 h and distances of 9.5 km. These travel speeds occurred when hatchlings were swimming in the same direction as westerly flowing currents that run parallel to the shore (figure 2). From the northwest, speeds of over 40 m min$^{-1}$ were not attained until after *ca* 5 h and displacement distances of 7.5 km with speeds of 54 m min$^{-1}$ attained after *ca* 7 h and distances of 10.5 km. These speeds occurred when hatchlings started to reach and travel with the NNW flowing currents (figure 2). Model current speeds in closest proximity (within *ca* 9 km) to the northwestern beach averaged $7.8 \pm 4.0$ m min$^{-1}$ and those in closest proximity to the southern beach averaged $5.5 \pm 2.2$ m min$^{-1}$. The fastest current flows were to the east of the island; averaging $14.4 \pm 2.7$ m min$^{-1}$ (electronic supplementary material, figure S1). During tracking periods from the southern nesting beach, wind direction was predominantly from the NE (range: NE–ENE) with wind speeds of between 8 and 20 knots. During tracking periods from the northwestern beach, wind direction was predominantly from the NE, however this was very variable, with periods when winds originated from the SE (less than or equal to 17 knots), east (less than or equal to 6 knots), north (less than or equal to 5 knots) and WSW–WNW (less than or equal to 5 knots).

### (b) Laboratory observations of the swimming frenzy

The swimming behaviours of 16 hatchlings (10 hatchery and six *in situ*) were assessed in the laboratory. Hatchlings swam

almost continuously during the first 24 h observation period (mean $\pm$ s.e. proportion of time period spent swimming: $0.78 \pm 0.04$), after this initial 24 h period, swimming activity significantly declined to around $0.43 \pm 0.02$ ($t = 8.95$, d.f. $= 13$, $p < 0.0001$) and then remained stable around 0.4 during the subsequent 24 h periods (figure 4*a*). This decline in swimming activity was due to a very diurnal pattern in swimming behaviour; while the mean proportion of diurnal hours hatchlings were active remained above 0.78 throughout the observation periods (figure 4*b*), the mean proportion of the nocturnal period spent swimming dropped significantly from $0.79 \pm 0.07$ on the first night to $0.11 \pm 0.04$ by the second night ($t_{13} = 12.84$, $p < 0.0001$) and then declined significantly again on the third night ($t_{15} = 4.60$, $p < 0.0001$) with hatchlings swimming for less than or equal to 0.01 during the third and subsequent nights (figure 4*c*). During daylight hours, the proportion of time spent swimming did not significantly decline at the $p < 0.001$ level between days. A LME model, revealed that in addition to the time period ($F_{6,48} = 36.43$, $p < 0.0001$), the daily proportions of time spent swimming during each 24 h period was also significantly related to the body mass of individuals ($F_{1,12} = 10.63$, $p = 0.007$); with larger individuals swimming longer than smaller individuals. Mean body mass of hatchlings was 19.32 g and ranged from 17.05 to 22.55 g. We found no swimming arena nor origin (*in situ* versus hatchery nests) effects on the proportion of time spent active ($F_{1,12} = 0.93$, $p = 0.35$ and $F_{1,12} = 0.08$, $p = 0.78$, respectively).

## 5. Discussion

The dispersal experiences of early life stages drive species population dynamics and the ontogeny of key life-history traits into adulthood [7,11,15]. However, *in situ* studies on the dispersal and behaviours of small cryptic organisms are difficult and hence there is a scarcity of knowledge surrounding this important life stage. With increasingly novel methods to study this 'lost' period now emerging, improving our understanding about the biological and physical
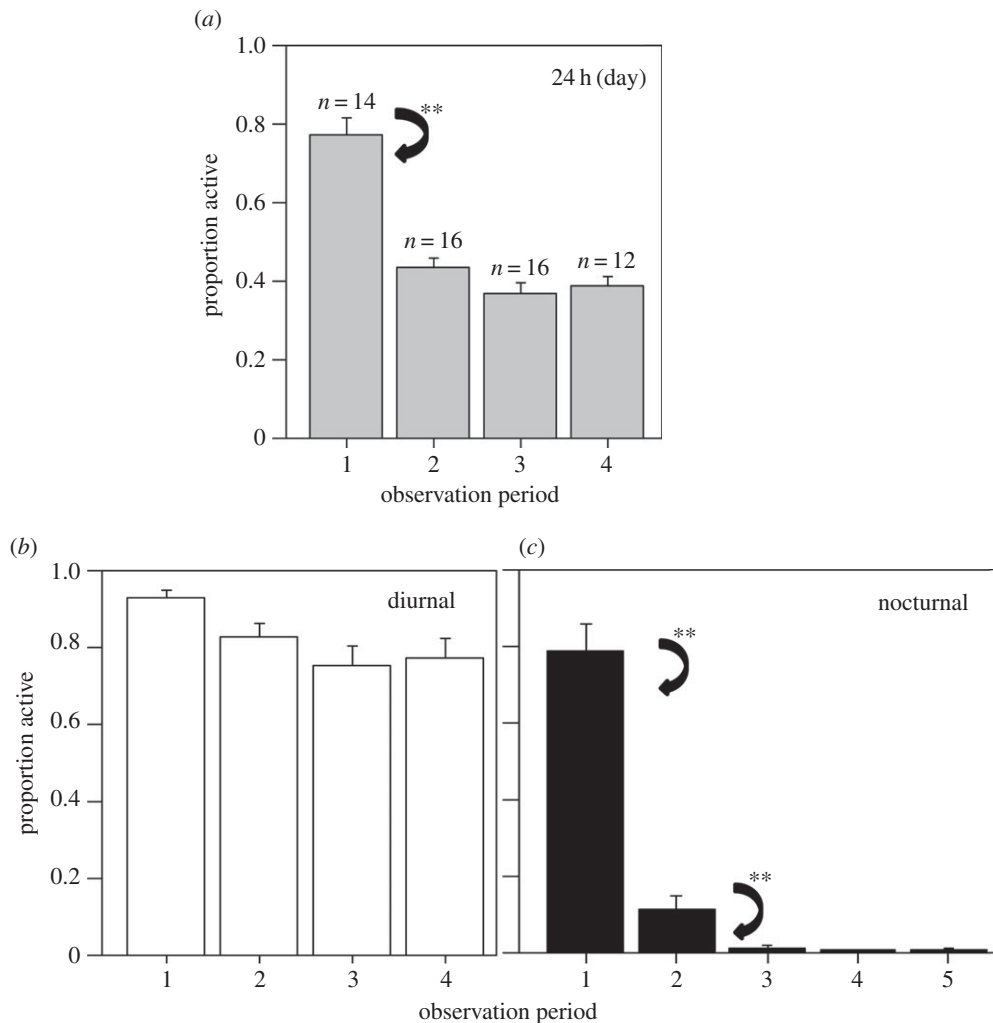
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**Figure 4.** Mean proportion of time spent swimming during each 24 h (daily) observation period (*a*) and each diurnal (*b*) and nocturnal (*c*) observation period where data were available for at least 12 hatchlings. Standard error bars are also plotted. Arrows indicate where swimming activity levels significantly differed between subsequent time periods at the $p < 0.0001$ level (**). Swimming activity dropped significantly after the first 24 h period due to the significant decline in nocturnal swimming activity after the first night and virtual nocturnal inactivity of hatchlings by the third night. Subsequent activity level patterns remained consistent for turtles kept up to 7 days with virtual nocturnal inactivity and the proportion of each diurnal period spent swimming remaining between 0.8 and 0.9.

determinants of dispersal and active swimming behaviours is crucial. This is particularly apparent for the conservation management of endangered species, like sea turtles as the habitats juveniles drift to shape adult habitat selections [11] where threats, like fishing, can be high [37]. Here, we expand on established laboratory and recently trailed novel *in situ* tracking techniques to address key knowledge gaps on the swimming behaviours of hatchling loggerhead sea turtles. In so doing, we directly observed the surface ocean current flows that drive the dispersal of hatchlings and indirectly assessed how these local flow conditions can shape the evolution of population-specific swimming frenzy behaviours. To our knowledge, this is the first time such immediate and rapid transport (approx. 60 m min$^{-1}$) of neonate hatchlings with surface ocean current flows has directly been observed in the field. Indeed, the rapid *in situ* tracking data provide compelling support that the population-specific swimming behaviours observed in the laboratory would have evolved in light of these local oceanic conditions.

The use of nano-tags as a means to track the movements of neonate flatback sea turtles (*Natator depressus*) was recently trailed [31], however stormy weather conditions limited active tracking durations to approximately 2 h. Here, we were able to track 11 individuals for up to *ca* 8 h and for distances

of up to 15 km. During tracking, the effects of surface ocean current flows were very apparent. Tracked hatchlings initially orientated offshore, however, within just a couple of hours, surface current flows were then the primary determinants of their subsequent swimming orientations, movement trajectories and travel speeds. Mean hatchling travel speeds more than doubled from initial speeds of *ca* 19–28 to *ca* 40–60 m min$^{-1}$ when hatchlings started to swim with prevailing current flows. While hatchlings reached these current flows quicker from the southern beach than the northwestern beach, prevailing ocean currents operating in these regions would then transport hatchlings from both locations broadly northwest and offshore to oceanic development habitats in the North Atlantic Gyre (e.g. figure 2*a*).

During the tracking period, the prevailing westerly and northwesterly surface current flows and large-scale process (such as Ekman drift) that our hatchlings encountered were realistically depicted in the ocean model (due to the assimilation of observational data). However, all models are limited in their spatial and temporal resolution. For example, our model used current flow values averaged over the 9 km grid scale and over 1 day of simulation and hence cannot account for small-scale variations and short-term fluctuations. Additionally, the direct effects of tides and wind on waves are not included in ocean

model simulations. The 'Stokes drift' effect, supplied by waves and swell [41], can result in stronger surface velocity flows than captured by the model. Our observed hatchling travel speeds, which were faster than predicted swimming and modelled flow speeds combined, thus highlight the role small-scale turbulence and wave/tide-induced motions (not represented or resolved by models) play in influencing their transport. These findings thus clearly highlight the strong necessity for increased *in situ* tracking studies [29,31] and the improved representation of mesco-scale features in the upper surface layer of models used to investigate drift patterns. Nonetheless, both *in situ* tracking and model flow data highlighted that hatchlings from this region do not have to swim far to reach favourable current flows that transport them away from predator-rich coastal areas to much safer oceanic development habitats.

Across the other side of the North Atlantic Ocean basin, in the southeastern USA, the World's second largest nesting population of loggerhead turtles exists. Nesting densities and hatchling survival predictions along the SE-USA coastline are positively correlated with the distance to favourable offshore currents associated with the Gulf Stream system [10,42]. Programming offshore swimming frenzy behaviours into drift simulations revealed that hatchlings would need to swim significantly less to increase their survival chances from regions closest (*ca* 29 km) to the most favourable offshore current flows (e.g. SE Florida), compared with regions where hatchlings had to traverse a large continental shelf (*ca* 250 km) before reaching these currents (e.g. SW Florida) [10]. Laboratory observations also revealed that neonate hatchlings from SW Florida swim for longer during the frenzy period than neonate hatchlings from SE Florida [22]. This was hypothesized to be an innate response associated with the distance of the Gulf Stream system from their natal areas [22]. Expanding on this work, we revealed that hatchlings from Boa Vista swam less than the hatchlings from both the SE and SW of Florida. While mean diurnal swimming activity levels were similar to the US hatchlings (with swimming levels sustained throughout a 6–7-day period at *ca* 70% of daylight hours), by the third night the mean nocturnal swimming activity of our turtles dropped from *ca* 80% to less than 1%, while hatchlings from SW Florida and SE Florida dropped from *ca* 87% and then remained between *ca* 30–50% and *ca* 4–19%, respectively.

Interestingly, in Boa Vista, *ca* 90% of turtle nesting occurs on the eastern half of the island [33] where the continental shelf is at its narrowest (less than 10 km; figure 1) and model-derived current flows were fastest (averaging more than 14.4 m min$^{-1}$; figure 2). Relatively little nesting activity occurs in the west and north of the island [33] where the shelf extends twice the distance and current flows were half the speed. Owing to the steep bathymetry around the volcanic Cape Verde Islands (figure 1), hatchlings from Boa Vista have to traverse a much shorter expanse of shallow water to reach the favourable offshore currents than populations from the USA. Cape Verde hatchlings would thus be expected to swim less than American hatchlings (as was observed) if local oceanic conditions shape the evolution of these swimming behaviours. Indeed, as hypothesized, by the third night Cape Verdean hatchlings were essentially inactive at night. It is now well documented that after the first 24 h of the frenzy period, hatchlings become increasingly less active at night [22,23]. The tendency towards an increasingly diurnal swimming activity pattern presumably helps to minimize predation risks as many oceanic predators are most

active during crepuscular/nocturnal periods [43,44]. Hence in regions, like Cape Verde, where hatchlings need to swim less to escape the predator-rich coastal realm and reach favourable currents, nocturnal inactivity is expected to be more pronounced. While differences between the experimental set-ups exist between studies, initial swimming activity levels of Cape Verdean hatchlings were similar to those observed in Florida [22]. Consequently, it seems unlikely that the subsequent nocturnal inactivity observed over the following days were artefacts of the experimental set-up, particularly as environmental conditions, like temperature and hatchling body mass were consistent between studies.

The observed positive correlation between hatchling body mass and swimming activity levels provides important new evidence that size may be a good fitness proxy for hatchlings. Given that nest temperature is thought to be negatively correlated with hatchling body size, climate change may thus exacerbate threats to sea turtles in more subtle ways than obvious threats like loss of nesting beaches and skewed sex ratios [45]. Additional evidence recently emerged that the swimming strengths of hatchlings are positively correlated to body size [45], these data in conjunction with our findings thus highlight that climate change may significantly impact the ability of hatchlings to reach favourable currents. This would be particularly detrimental in regions, like the SE-USA, where hatchlings have to traverse a large predator-rich continental shelf before reaching flows that transport them to much safer oceanic development areas.

Our observations of the rapid transport of hatchlings with ocean currents flows that pass within 10 km of the island of Boa Vista and population-specific swimming behaviours (e.g. nocturnal inactivity) provide further support for the hypothesis that local oceanic conditions drive the evolution of local innate swimming behaviours of hatchling sea turtles. Consequently, emerging evidence for locally evolved swimming behaviours highlights the need for considerations of local oceanic conditions to better inform the general parametrization of swimming behaviours into modelled dispersal simulations. For species like sea turtles where juvenile mortality rates and behaviours are shaped by local oceanic conditions, one would expect a strong selective pressure for surviving individuals to return to breed at the sites they were born. Advantages to philopatry occur when population-specific genomic/epigenomic regions that influence the swimming behaviours of hatchlings are optimized to the local oceanic conditions. This pattern is consistent with the observed philopatric behaviour of Cape Verde loggerhead turtles and the maintenance of locally adapted genetic make-up [35]. Furthermore, a strong genetic basis to inherited migration behaviours such as travel directions and activity levels are now well documented among a range of other first-time migrants [46]. For sea turtles, parental investment stops when adults finish nesting. Inherited behaviours that guide first-time migrants to favourable currents for their dispersal will thus be under strong selection in the absence of learning opportunities from their mothers/more experienced conspecifics (e.g. as is the case in social migrants) [47,48].

Until techniques to track neonate hatchling turtles (*ca* 20 g) over extended periods exist, it remains difficult to assess the ontogeny of the initial observed swimming behaviours of hatchlings which are thought to become stronger but more passive swimmers [28]. Consequently, the ability to accurately parametrize these behaviours into ocean model simulations

across the spatial and temporal scales they disperse remains compromised. To date, the smallest turtles that have been fitted with satellite tags are captive reared (3.5–9-month-old) juvenile loggerhead turtles weighing 300–720 g [49]. With increasing technological advances and novel laboratory and field approaches to monitor the swimming behaviours of small cryptic organisms [19,21,22,31], obtaining more accurate data on the swimming behaviours of small organisms is now considered a priority that is anticipated to have great conservation utility. This is particularly apparent in light of recent evidence that (i) small amounts of active movements of small organisms in strong current flows may significantly alter their dispersal outcomes [10,16,17,50,51] and (ii) the dispersal of early life-history stages has significant conservation implications by driving the subsequent ontogeny of adult habitat selections, behaviours and the population dynamics of endangered species [6,7,11]. Finally, empirical studies of this nature will be crucial in the development of accurate multidisciplinary models that combine advances in *in situ* tracking technologies with increasingly powerful oceanographic, stable isotopes and genetic *in silico* tools to elucidate ocean-scale ecological patterns across multiple life-histories stages and species of conservation concern.

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