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Ocean currents, individual movements and genetic structuring of populations

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Abstract Ocean currents profoundly impact all life in the oceans and over a broad size spectra species may show both horizontal and vertical movements to stay on preferred locations. As a corollary it might be expected that individuals in preferred oceanic habitats may simply drift with flows. We explored these scenarios by both satellite tracking young pelagic loggerhead turtles and examining the genetic structuring of individuals on coastal foraging areas across the Mediterranean in relation to ocean flows measured both with Lagrangian drifters and a numerical ocean circulation model for the area. Both patterns of movement ($n = 18$ turtles ranging in size from 41.2 to 68.5 cm CCL tracked for up to 460 days) and genetic structuring ($n = 165$ individuals from six sites across the ocean basin) suggested that ocean flows profoundly impact the movements of immature turtles and suggest a pattern of largely passive drift within an ocean basin that, throughout, is broadly favourable for developing loggerhead turtles. The situation contrasts with more heterogeneous habitats in the Atlantic and Pacific, where larger amounts of directional swimming may be required to avoid sub-optimum areas.

Introduction

Environmental flows (winds and currents) impact the movements and distribution of a broad range of species varying in size from insects and plankton up to mega-fauna such as whales and turtles (Chapman et al. 2011; Fossette et al. 2015; Hays 2017). How animals deal with these flows is a key unresolved question in movement ecology (Hays et al. 2016). Extensive studies with insects and birds have revealed these groups may select when to fly and selectively use favourable winds (e.g. Chapman et al. 2008; Felicísimo et al. 2008). In contrast in marine environments, particularly oceanic zones, animals live in their moving environment and hence may be continuously subjected to flows which may be favourable (e.g. maintaining organisms in suitable areas or carrying them toward favourable areas) or unfavourable. At the small end of this size spectrum, organisms with short generation times, such as bacteria, may evolve as they are advected by currents, leading to rapid selection for new strains and species to fit local conditions (Hellweger et al. 2015). However, for larger long lived species two scenarios exist: first animals can move independently of currents or alternatively animals may drift passively.

An a priori expectation is that active directed movements, which may be energetically costly, will occur where they convey benefits, for example helping animals stay within or move towards preferred areas (Fossette et al. 2012). For example, directed movements independent of currents have recently been shown to reduce the chances of jellyfish stranding ashore (Fossette et al. 2015). Conversely, where

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there is no benefit to active directed swimming, then passive drift might be expected. Long-term tracking of some species seems to support these expectations and show evidence of behavioural switching at different times. For example, adult leatherback turtles that forage in the open ocean show directional swimming to move away from their breeding grounds but then seem to drift passively when they encounter areas of high food availability (Luschi et al. 2006; Doyle et al. 2008).

Ocean currents will always provide some contribution to the movement of sea turtles, with their overall pattern of movement reflecting the sum of active swimming plus current drift. The relative importance of active swimming versus current drift in influencing the pattern of movement may, however, change massively depending on the size and swimming ability of turtles as well as their motivation to swim actively. The quantification of benefits of different movement strategies remains a challenge (Hays et al. 2016). For sea turtles it is generally assumed that hatchlings, which are only a few cm long, will have movements that are strongly influenced by ocean currents (Polovina et al. 2006; Scott et al. 2012; Putman et al. 2012; Mansfield et al. 2014; Briscoe et al. 2016) while adults, which can be 1 m or more in length, can swim independently of currents (Luschi et al. 2003, 2006; Bentivegna et al. 2007; Hays et al. 2010; Hawkes et al. 2011). However, small weakly swimming animals could very quickly find themselves in a bad location they cannot move out of and may need to expend energy actively swimming to maximize chances of avoiding such a fate; in contrast, stronger swimmers may not need to expend energy consistently, because if conditions become unfavourable they could easily swim to somewhere better (Fossette et al. 2015).

How the ontogeny of swimming ability develops has recently been illuminated by the elegant use of small electronic tags deployed on hatchlings (Scott et al. 2014a) and early juveniles (Mansfield et al. 2014; Putman and Mansfield 2015; Briscoe et al. 2016; Christiansen et al. 2016). Direct tracking has revealed how young loggerhead turtles *Caretta caretta* only 11–30 cm in length can move independently of currents on the short, although in the end they remain within the core area predicted by numerical simulation and passive drifters (Mansfield et al. 2014; Putman and Mansfield 2015). Likewise, laboratory experiments have revealed that hatchling turtles exhibit small amounts of active directional swimming to avoid advection to unfavourable areas, but swimming is not geomagnetically oriented within favourable range limits (Lohmann et al. 2001; Putman et al. 2015).

Satellite tracking of larger juvenile turtles 20–40 cm in the Pacific Ocean has shown regionally tuned directional swimming, which reflects a combination of their swimming ability and their response to the detection of sub-optimum areas (Abecassis et al. 2013; Christiansen et al. 2016). However, we might expect young turtles that are already in preferred areas might simply drift passively, particularly in the case of juvenile turtles 40–60 cm. Individuals within this size range are powerful swimmers (Revelles et al. 2007b) and can easily swim away from unfavourable areas if advected there. This may explain why in the North Pacific Ocean juvenile turtles that size swim more slowly, both in absolute and relative terms, than their smaller conspecifics (Abecassis et al. 2013).

To examine the possibility that young turtles 40–60 cm that are already in preferred areas might simply drift passively and assess whether ocean currents predict large-scale patterns of distribution, we both satellite tracked young pelagic loggerhead turtles in the Mediterranean Sea and examined the genetic structuring of individuals on coastal foraging areas and compared these patterns to ocean flows measured both with Lagrangian drifters and a numerical ocean circulation model for the area. If juvenile turtles are engaged into active swimming only to avoid sub-optimum areas, (1) their dispersal patterns at broad scale are expected not to differ from those of Lagrangian drifters and virtual particles and (2) the genetic structuring of juvenile foraging grounds is expected to match that resulting from the passive drift of hatchlings revealed by virtual particle tracking studies (Hays et al. 2010; Casale and Mariani 2014).

Materials and methods

Genetic structuring

Garofalo et al. (2013) and Clusa et al. (2014) reported the haplotype frequencies of juvenile loggerhead turtles from foraging grounds off Israel, eastern Italy, southern Italy, Malta, western Italy, eastern Spain and the Balearic Islands (Fig. 1), most of them incidentally caught by fishermen. Although a diversity of mitochondrial markers has been reported for Mediterranean foraging grounds, only the haplotypes derived from the amplification of an 815 bp fragment of the mtDNA control region have been considered for the present study, because differences within Mediterranean rookeries relied primarily in the frequency of haplotypes CC-A2.1, CC-A2.8 and CC-A.9 (Clusa et al. 2013).

Haplotype frequencies were recalculated after the removal of individuals of Atlantic origin (Garofalo et al. 2013; Clusa et al. 2014). Firstly, those carrying haplotypes exclusive from Atlantic rookeries were easily identified and removed. Secondly, the number of individuals of Atlantic origin carrying shared haplotypes with Mediterranean rookeries (CC-A2.1 and CC-A3.1) was estimated considering the haplotype frequencies reported by Carreras et al. (2011) for the Atlantic stock arriving into the Mediterranean Sea: 22 CC-A1.1, 2 CC-A1.3, 28 CC-A2.1, 4 CC-A3.1, 3 CC-A14.1 and 4 CC-A31.1. This procedure

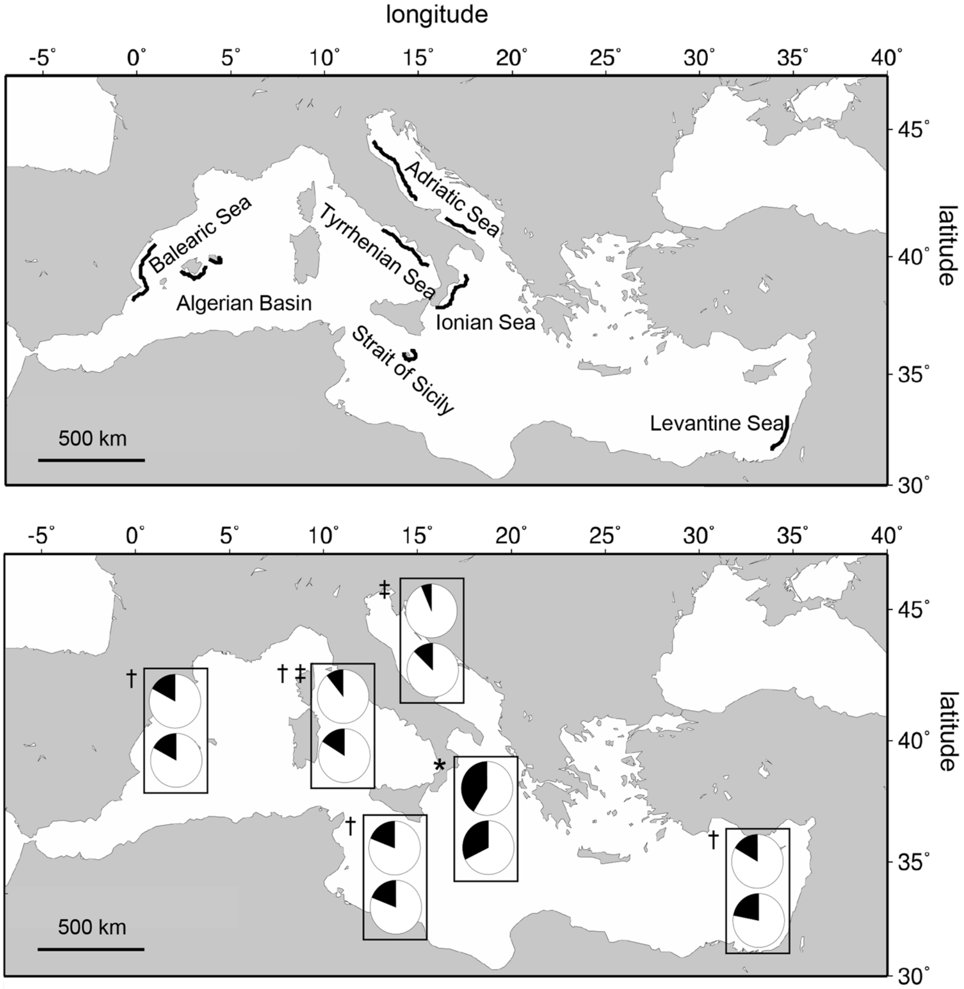

Fig. 1 Coastlines surveyed for the genetic characterization of foraging grounds (top panel) and proportions of haplotype CC-A2.1 (white) and other haplotypes (black) in each foraging ground (bottom panel). The top pie-chart within each box shows the observed proportions of haplotypes within the foraging ground, and the bottom pie-chart, the expected proportions according to a drifting model. Boxes sharing the symbols to the left do not differ in the proportions of observed haplotypes (Chi-square test)

was used in Israel, western Italy, eastern Spain and the Balearic Islands, but sample size was reduced to only 17 turtles of Mediterranean origin in the Balearic Islands and hence that foraging ground was finally excluded from later analysis. Only Mediterranean and shared haplotypes had been reported for eastern Italy, Malta and southern Italy, but direct assignation with nuclear markers (Piovano et al. 2011) and Mixed Stock Analysis (Clusa et al. 2014) had revealed the presence of a few individuals of Atlantic origin. Accordingly, individuals with shared haplotypes were removed according to the contribution of Atlantic rookeries to the juveniles in eastern and southern Italy.

Once juveniles of Atlantic origin had been removed from the data set, the haplotype frequencies in the six foraging grounds remaining (Israel, eastern Italy, southern Italy, Malta, western Italy and central-eastern Spain) were compared using a Chi-square test. Furthermore, the Chi-square test was used to compare the haplotype frequencies in each foraging ground with those expected according to the origin of the hatchlings present into each sub-basin as indicated by a previous virtual particle tracking experiment (Table A1) and nest counts and haplotype frequencies in major Mediterranean rookeries (Table A2).

Virtual particle tracking

We used the web-tool Connie 2 (http://www.csiro.au/connie2/) to answer questions such as: (1) which regions were most likely visited by juveniles at foraging grounds prior to sampling, assuming they dispersed with currents, (2) where would juvenile turtles released in the Balearic Islands most probably go if dispersed as drifting particles, and (3) can turtles drift from the eastern to the western Mediterranean along the Strait of Sicily? Connie 2 uses archived currents from oceanographic models and virtual particle tracking techniques to estimate connectivity statistics from user-specified source regions (or to user-specified sink regions). The Mediterranean Sea Reanalysis (MEDREA) was developed using the OPA 8.1 code for the Mediterranean Sea and adjacent North Atlantic Ocean region, which forms part of the Mediterranean ocean Forecasting System (MFS). The data assimilating model has 1/16th degree horizontal resolution and includes realistic evaporation and river discharges. The current version of the reanalysis covers the period 1985–2007. Virtual particles were seeded within the user-specified source (or sink) region at a constant rate of 25 particles per grid cell per day over variable periods (see below). They were subsequently tracked individually for using a fourth-order Runge–Kutta ODE solver that linearly interpolates in time and horizontal space to find the horizontal velocity at the required depth and time.

To assess the most likely sources of the particles arriving at the regions sampled to study genetic structuring, we released virtual particles at a point central to each sampling area from June 6th to July 7th, 2006, and back-tracked them for 365 days. To assess the region to where turtles released in the Balearic Islands most probably go if drifted passively, we released virtual particles south to Formentera Island from March 1st to April 30th 2005, and tracked them for 180 days to reproduce the average release date and site of the turtles satellite tracked in the area (Cardona et al. 2005; Revelles et al. 2007a, c). This is critical, because the results of virtual particle experiments are highly sensitive to the start location, start date and tracking duration (Putman et al. 2016). Finally, to assess the possibility that passive drifting turtles travel from the eastern Mediterranean to the western Mediterranean, we released virtual particles at the western part of the Strait of Sicily (37.365 N 11.725 E) for a month (June 6th to July 6th) annually from 1985 to 2007 and tracked them for 180 days. Due to the temporal limitation of the model, particles released on 2007 were tracked for only 150 days.

Turtle and drifter tracking

We compared the movement of 18 loggerhead sea turtles satellite tracked in the western Mediterranean from 2003 to 2007 (Table A3) with that of 17 Lagrangian drifters released from 2000 to 2013 in the same region (Table A4). Turtle tracks were selected from those previously reported by Cardona et al. (2005), Revelles et al. (2007a, c), Cardona et al. (2009) and Cardona et al. (2012). Most of them had been captured by hand, but a few have spent some time in rescue centres. Three rehabilitated turtles exhibiting anomalous behaviour (Cardona et al. 2012) and four turtles spending most of the tracking time on very shallow areas (Cardona et al. 2009) were excluded from the study, as the focus was on turtles foraging pelagically in the ocean realm. Lagrangian drifters deployed in the western Mediterranean and spending most of the tracking time within the Balearic and Algerian basins were selected from the Global Lagrangian Drifter Data (http://www.aoml.noaa.gov/envids/gld/), as turtles remained in those two sub-basins during the whole tracking period.

Data from Lagrangian drifters and turtles were interpolated to provide with one position every 24 h and hence produce two comparable data sets. Animal movement is often characterized by turning angles and step length, with in turn is a function of the speed of travel (Bovet and Benhamou 1988). Here we are interested in testing the null hypothesis that turtles spread from the release point at the same rate than drifters do and hence aim to combine both parameters. To do so, we have computed the speed of spread, i.e. the ratio of travelled distance from the release point to travel time. In this way, speed of travel and turning angle and integrated into a single parameter that measures how fast turtles and drifters move away from the release point. We also computed the daily change in latitude (Δ latitude) and longitude (Δ latitude) with respect to the deployment point. We used General Linear Models, as implemented in IBM SPSS Statistics 24, to assess the effect of deployment year and platform type (Lagrangian drifters vs. turtles) on the variability of the above reported movement descriptors. Following Putman and Mansfield (2015) and Briscoe et al. (2016), we also used a series of Mann–Whitney *U* tests to test whether distance to the release point, |Δ latitude|, and |Δ longitude| differ between drifters and turtles at 20, 40, 60, 80, and 100 days.

A second set of 30 Lagrangian drifters were deployed in the Strait of Sicily from 2005 to 2007 (Table A5) and were used to test the hypothesis that eastward drift along the Strait of Sicily is sometimes possible, as suggested by virtual particle tracking experiments using Connie 2.

Results

Genetic structure

Haplotype CC-A2.1 prevailed at the six juvenile foraging grounds considered (Fig. 1 and Table A6), but statistically significant differences existed between the haplotype frequencies in some of them (Fig. 1 and Table A8). Southern Italy differed from any other foraging ground analyzed, because of the very high frequencies of CCA2.9 and CCA3.1. Eastern Italy also differed from any other foraging ground, except western Italy, because of the extremely low frequency of haplotypes other than CC-A2.1. Finally, no significant difference was found among Israel, Malta, western Italy, and eastern Spain. Overall, these results indicated a differential contribution of Mediterranean rookeries to the foraging grounds considered, thus ruling out the homogenous admixture of juveniles from Mediterranean rookeries all over the Mediterranean seas.

Connie 2 was used to check the correspondence between the foraging grounds actually sampled by Garofalo et al. (2013) and Clusa et al. (2014) and the sub-basins identified by Casale and Mariani (2014) in their virtual particle tracking experiments. Results showed that particles arriving to the coastal regions of eastern Italy and Israel sampled by Clusa et al. (2014) come from the whole Adriatic Sea and the south Levantine Sea, respectively, with negligible contributions from other sub-basins (Fig A1). Accordingly, the haplotype frequencies reported for juveniles in those areas were compared with those expected for the Adriatic Sea and the Levantine Sea (Table A7). Conversely, Connie 2 showed that particles arriving to southern Italy had mixed origins, mainly in the northern Ionian Sea and the southern-central Mediterranean Sea and also from the western Mediterranean (Fig A1). Accordingly, the haplotype frequencies observed in juvenile turtles from southern Italy were compared with those expected for combination of the haplotype frequencies expected for the Ionian Sea and the southern-central Mediterranean in proportions 1:3 (Table A7). Finally, Connie 2 revealed that particles drifting from the eastern Mediterranean to Malta came mainly from the Strait of Sicily, a region supposed to receive hatchlings only from rookeries in western Greece, Crete and Libya according to Casale and Marianni (2014).

Although haplotype CC-A2.1 was expected to prevail everywhere, sub-basins were expected to differ in the relative frequency of haplotypes CC-A2.9 and CC-A3.1 (Fig. 1 and Tables A6 and A7). The former was expected to be the second most frequent haplotype in the southern-central Mediterranean Sea and the later more frequent in the Levantine and southern-central Mediterranean Sea than anywhere else. Differences between observed and expected frequencies were not statistically significant for any foraging ground (Fig. 1 and Table A8).

Turtle and drifter movement

The tracks of instrumented turtles were highly convoluted and turtles spent most of the tracking time within the Algerian Basin (Fig A2). Drifters released in the western Mediterranean also followed rather convoluted routes and usually become involved in loops that retained them within the release area for several weeks (Fig A3). Tracks straightened only off the coasts of northern Africa and southern France, where the speed of travel increased. As a consequence of convoluted routes, the average speed of travel was much larger than the average speed of spread, both for turtles (speed of travel: 0.57 ± 0.18 km h^{-1}; speed of spread: 0.20 ± 0.11 km h^{-1}; $t = 8.594$, $df = 17$; $p < 0.001$) and drifters (speed of travel: 0.62 ± 0.22 km h^{-1}; speed of spread: 0.30 ± 0.27 km h^{-1}; $t = 7.407$, $df = 16$, $p < 0.001$).

Figure 2 summarizes the movement of turtles and drifters from the release point during the first 110 days of tracking. The broader 95% CI of drifters, as compared with those of turtles, certainly reflected a much broader scatter of release points within the western Mediterranean. However, GLMs revealed no statistically significant effects of deployment year and type of platform (Lagrangian drifters vs. turtles) on average speed of spread ($F_{\text{model}} = 2.354$, $p = 0.111$), Δ latitude ($F_{\text{model}} = 2.341$, $p = 0.112$), |Δ latitude| ($F_{\text{model}} = 0.298$, $p = 0.744$) and Δ longitude ($F_{\text{model}} = 0.493$, $p = 0.616$). Deployment year, but not type of platform, had a significant effect on the speed of travel ($F_{\text{model}} = 3.401$, $p = 0.046$; $F_{\text{year}} = 6.141$, $p = 0.019$; $F_{\text{platform}} = 3.120$, $p = 0.087$) and |Δ longitude| ($F_{\text{model}} = 10.386$, $p < 0.001$; $F_{\text{year}} = 13.330$, $p < 0.001$; $F_{\text{platform}} = 0.943$, $p = 0.339$). The effect of deployment year on those parameters is likely the result of differences in the latitude of drifter release: usually north to 40ºN before 2012 and south to 40ºN latter. Sequential Mann–Whitney tests revealed no difference on travelled distance and |Δ longitude| at 20, 40, 60, 80 and 100 days. They revealed statistically significant differences on |Δ latitude| at 20 days, but not latter (Table 1).

Connie 2 revealed that after 6 months, most of the particles released in the southern Balearic Islands will remain in the Algerian Basin and the Balearic Sea (Fig. 3). This result highly agreed with the dispersal of satellite tracked turtles, as they remained most of the time within the Algerian Basin, with only a few short incursions into the Balearic Sea (Fig. 3). The accumulated probabilities that a particle or a turtle stayed in each 1° × 1° cell during the tracking period were positively and significantly correlated (Spearman Rho = 0.580, $p < 0.001$).

Finally, 13 of the 30 Lagrangian drifters released in the Strait of Sicily drifted eastward to the Ionian or the central-southern Mediterranean Sea, 14 remained within the area during tracking and 3 drifted westward, into the Tyrrhenian Sea, although 2 of them moved again into Strait of Sicily after a few weeks (Table A5). Connie 2 confirmed the prevalence of eastward flowing along the Strait of Sicily, but also a significant westward flow into the western Mediterranean in 1986, 1988, 1992 and 2008 and a much limited westward flow in 1987 and 2005 (Fig A4).

Discussion

The results reported here strongly suggest that in the Mediterranean Sea young loggerhead turtles ranging 41–69 cm CCL drift passively in ocean currents at large spatial (hundreds of kilometres) and temporal (from months to years) scales. Laboratory findings have shown directional or non-directional swimming in loggerhead turtles related to the geomagnetic field (Lohmann et al. 2001; Putman et al. 2015), while recent tracking of free-living juveniles has shown evidence for directional swimming in the Gulf of Mexico (Putman and Mansfield 2015) and the Pacific Ocean (Abecassi et al. 2013; Christiansen et al. 2016). Taken together, these findings point to behavioural plasticity in these species, with directional swimming or passive drifting

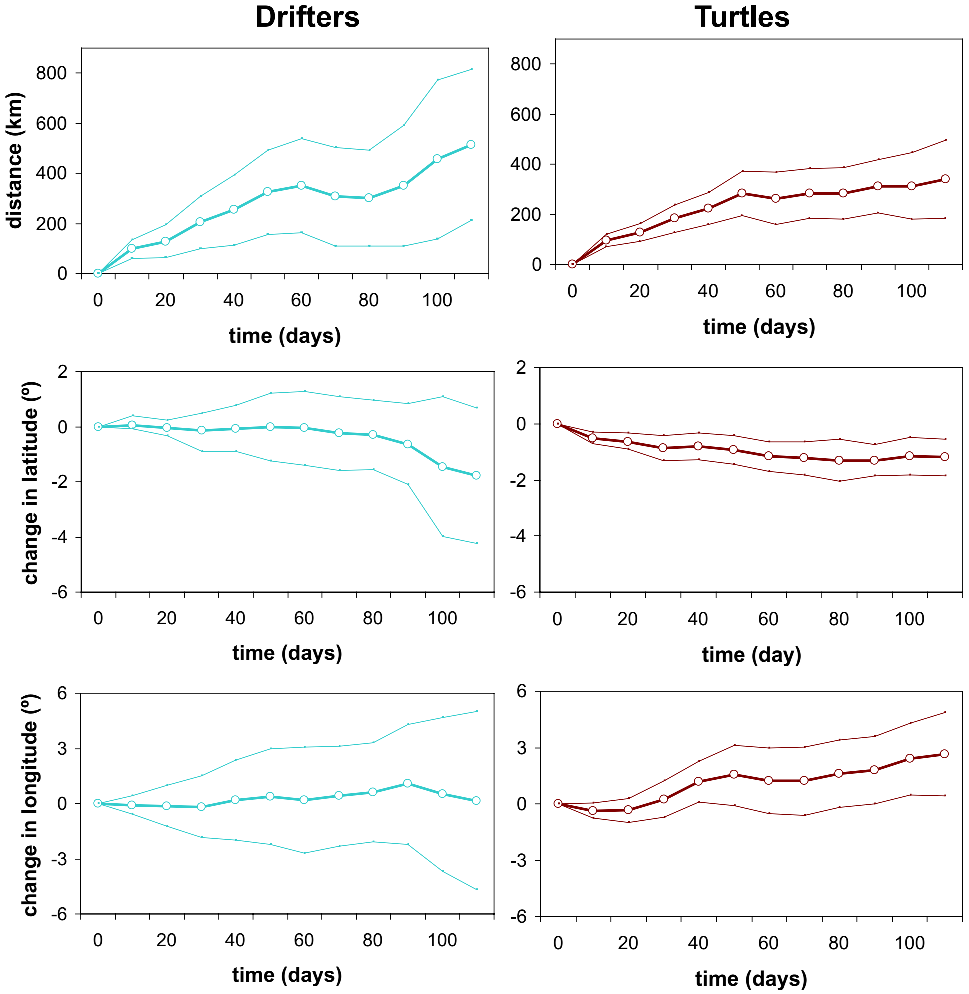

Fig. 2 Metrics summarizing the movement of drifters and turtles during the first 110 days after release: distance traveled (top), change in latitude (center) and change in longitude (bottom). Population average is shown by thick lines, and thin lines show the 95% CI. GLM revealed no significant effects of type of platform (drifters vs. turtles) on average speed of spread, daily change in latitude and daily change in longitude

being tuned to local conditions. This conclusion is based on three different pieces of evidence. Firstly, the genetic structuring at juvenile foraging grounds retains the haplotype frequencies expected from the passive drift of hatchlings from nesting beaches according to virtual particle diffusion models, a result reminiscent of similar findings noted for some plankton (Lee et al. 2013) and green turtles (Putman and Naro-Maciel 2013). Secondly, satellite tracked juvenile turtles spread from the release point at the same velocity than drifters do. Thirdly, satellite tracked turtles remain in the same region than virtual particles after 6 months of tracking. Taken together our observations and those of others (Mansfield et al. 2014; Putman and Mansfield 2015; Christiansen et al. 2016) show tuning of movement behaviour in pelagic turtles akin to the tuning of flying behaviour seen in birds and insects in relation to favourability of winds. This commonality of behavioural tuning highlights the profound impact of environmental flows on the evolution of movement behaviour across diverse taxa.

However, the tight links between currents and the movement of juvenile turtles larger than 40 cm CCL are certainly not because they drift mercilessly in the surface of the oceans. The average speed of travel of the drifters tracked for this study (0.6 km h^{-1} or 17.3 cm s^{-1}) was much lower than the critical swimming velocity of turtles within the size range considered here (Revelles et al. 2007a). Indeed, juvenile loggerhead turtles in the Mediterranean similar in size to those here studied have been reported to be involved in directional swimming (Hochscheid et al. 2010; Casale et al. 2012) and we are aware that even smaller turtles are capable of directed movements in the open ocean (e.g. Mansfield et al. 2014; Putman and Mansfield 2015). Unfortunately, our approaches are unlikely to resolve movement independent of flows at small spatial (a few kilometres) and temporal scales (a few days). In this instance even simultaneous deployment of Lagrangian drifters with tracked turtles might be criticized as drifters and turtles may be subjected to flows at slightly different depths and different levels of windage. The point here is that drifters and turtles may differ in their movements at small temporal and geographic scales because they experience different short term conditions, but in the long run and over broad areas, they may not differ in general

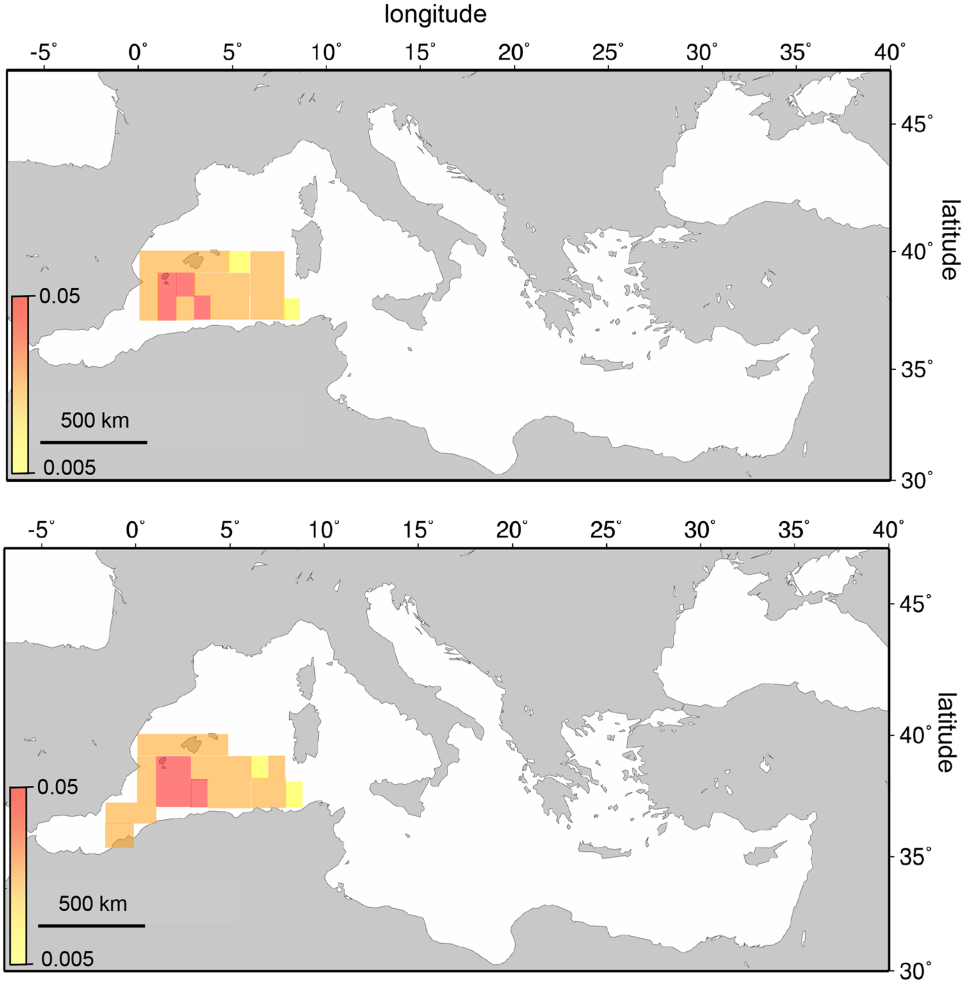

Fig. 3 Dispersal after 180 days of virtual particles (top) and instrumented loggerhead turtles (bottom) released off Formentera Island. Colours denote the accumulated probability that a particle or a turtle stays in each 1° × 1° cell during the tracking period

movement patterns if turtles do not avoid sub-optimal areas. Furthermore, within a day or two the drifters and turtles will no longer be together so then there is no way of assessing the currents where the turtles are, a situation than may even worsens if the stress induced by capture and handling alters turtle behaviour during a few hours or days after release. These behavioural anomalies may explain why turtles travelled broader than drifters immediately after release for this study but remained within the same broad areas after several months.

Recently Putman et al. (2016) advocated for analysing ocean currents along the tracks of drifters to test how well the modelled ocean velocities can resolve the movement of a known passive drifter and along the tracks of animals to draw conclusions as to whether movement can be accounted by ocean currents alone. Here we opted not to analyse our data from that perspective because we are asking whether ocean currents predict large-scale patterns of distribution and do not aim to resolve individual tracks. Ultimately to resolve the question at this level, direct measurement of movements in relation to flows will be needed, for example by recording the heading and swim speed of turtles compared to their movement over the ground. Such technical developments should now be possible with the broad development of equipment for animal biotelemetry (Rutz and Hays 2009), although resolving the ocean velocities experienced by individual organisms remains a problem (Putman et al. 2016).

Water temperature may have a deep impact in the activity patterns of marine turtles, as they often modify their behaviour to thermoregulate (Fossette et al. 2012). Avoiding cold water is likely one major reason for the directional swimming of juvenile loggerhead turtles in the Pacific Ocean (Polovina et al. 2000, 2004; Abecassis et al. 2013) and the North Atlantic Ocean (Lohmann et al. 2001; Mansfield et al. 2014; Putman et al. 2015). The situation is different in the Mediterranean Sea, where winter temperature is usually above 13 °C and differences in sea surface temperature are usually less than 5° C across the whole basin at any time. In this scenario, thermoregulation is an unlikely reason for the directional swimming of loggerhead turtles, except to avoid the northernmost parts of the basin in winter (Luschi and Casale, 2014). On the other hand, sea surface temperature is a poor predictor of swimming velocity in wild turtles (Revelles et al. 2007a; Putman and Mansfield 2015).

After living in oceanic areas for many years, loggerhead turtles may take up residence in coastal foraging sites and feed on the seabed in fixed areas throughout their late juvenile and adult lives (Avens et al. 2003; Broderick et al. 2007; Schofield et al. 2010). So finding suitable settlement habitats may be a second major force causing directional swimming in juvenile loggerhead turtles. While there is strong evidence that juvenile sea turtles may settle in foraging grounds they encounter during their oceanic drifting (Ceriani et al. 2012; Eder et al. 2012; Pajuelo et al. 2012; Schofield et al. 2013; Cardona et al. 2014; Scott et al. 2014b), there is a ceiling for the maximum reproductive migration distance for adult sea turtles (Hays and Scott, 2013). Hence juveniles that have drifted far (many 1000 s of km) from their natal sites, may show directional swimming to return closer to these natal sites prior to taking up a coastal residence. Examples of this directional swimming include loggerheads travelling westwards across to Pacific to return closer to their natal sites in Japan and loggerhead travelling westwards across the Atlantic to return to natal sites in eastern USA or Caribbean (Polovina et al. 2000, 2004; Cejudo et al. 2006; Eckert et al. 2008; Revelles et al. 2008; Briscoe et al. 2016). The need to travel westwards, independently of currents, may explain why the swimming velocity of juvenile turtles in the North Pacific Ocean increases when they become larger than 60 cm (Abecassis et al. 2013). In contrast, the Mediterranean is a fairly small ocean basin, so adult reproductive migrations back to natal breeding sites is possible from throughout the basin and the scarcity of adults foraging into the western Mediterranean (e.g. Schofield et al. 2013; Cardona et al. 2014) simply reflects the limited access of juveniles to that sub-basin (Casale and Mariani 2014) because of the prevalent eastward flow at the Strait of Sicily. Hence, in contrast to the Atlantic and Pacific, there may be no need for juveniles in the Mediterranean to show directional swimming to return closer to natal sites. This may explain why the behaviour of the four turtles considered here larger than 60 cm CCL was not different from that of the smaller individuals, although they might be in a rather different stage of their life cycle.

In conclusion, although juvenile turtles may be involved in small scale movements independent of currents, multiple lines of evidence suggest that ocean flows profoundly impact the movements of juvenile turtles in the Mediterranean Sea and suggest that surface advection is dominant in determining the paths of turtles within an ocean basin that, throughout, is broadly favourable for developing loggerhead turtles. The situation contrasts with more heterogeneous habitats in the Atlantic and Pacific, where larger amounts of directional swimming may be required to avoid sub-optimum areas.

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Compliance with ethical standards

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Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This article is based on previously published data and does not contain any studies with animals performed by any of the authors specifically for this article.

Data accessibility Data from turtles are in the Dryad repository (http://www.datadryad.org; doi:10.5061/dryad.9hn0m). Data from Lagrangian drifters are available at http://www.aoml.noaa.gov/envids/gld/.

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