

Ontogenetic development of migration: Lagrangian drift trajectories suggest a new paradigm for sea turtles

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Long distance migration occurs in a wide variety of taxa including birds, insects, fishes, mammals and reptiles. Here, we provide evidence for a new paradigm for the determinants of migration destination. As adults, sea turtles show fidelity to their natal nesting areas and then at the end of the breeding season may migrate to distant foraging sites. For a major rookery in the Mediterranean, we simulated hatchling drift by releasing 288 000 numerical particles in an area close to the nesting beaches. We show that the pattern of adult dispersion from the breeding area reflects the extent of passive dispersion that would be experienced by hatchlings. Hence, the prevailing oceanography around nesting areas may be crucial to the selection of foraging sites used by adult sea turtles. This environmental forcing may allow the rapid evolution of new migration destinations if ocean currents alter with climate change.

Keywords: AOML; drifter; Argos; Fastloc; GSM; Mediterranean currents

1. INTRODUCTION

Long distance migration is a widespread feature in terrestrial and marine systems and has inspired decades of research into, for example, the adaptive significance of migration, navigational cues employed, behaviours used to optimize travel and how individuals learn migration routes (Alerstam *et al.* 2003; Alerstam 2006; Dingle & Drake 2007). Pioneering experiments with starlings in the 1950s suggested that migrating birds are born with an innate compass heading to follow in their first migration, and then as they complete subsequent trips their map sense develops and they are able to compensate better for unexpected displacements (Perdeck 1958). Similarly, in many insects an innate compass sense is probably central to migration trajectories (Chapman *et al.* 2008*a,b*). In other groups, such as some fishes, social learning may be important (Galef & Laland 2005). However, in some other taxa, the processes that shape migration routes and destinations remain enigmatic, with a case in point being sea turtles and some fishes (Sims *et al.* 2003). Sea turtles have long been considered paradigmatic long-distance

migrators (Darwin 1873), often travelling hundreds or thousands of kilometres between breeding and foraging sites (Luschi *et al.* 2003). Molecular evidence has convincingly demonstrated that turtles generally show good fidelity to the beaches where they hatched (Lee 2008) and similarly adults, certainly for some species, show good fidelity to foraging sites (Broderick *et al.* 2007). However, what drives the initial selection of these foraging sites is not known.

It has been well described how hatchling turtles, because of their limited swimming and diving abilities coupled with positive buoyancy, probably drift passively with ocean currents at the ocean surface, at least in the early part of their lives (Carr & Meylan 1980; Bolten *et al.* 1992; Hays & Marsh 1997). Yet, the importance of these initial drift scenarios for the subsequent behaviour of adult turtles has received little attention. Here, we develop a hypothesis that the foraging sites used by individual sea turtles may not solely reflect innate behaviours or social learning, but instead may reflect their previous experiences as hatchlings and young juveniles when they are carried by ocean currents. As such, sea turtles may represent a new paradigm for the ontogenetic development of migration routes.

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Table 1. Attachment details for tracked adult turtles. Data for turtles A–G are from Zbinden *et al.* (2008). Turtles 4394 and 15119_07 are described in Schofield *et al.* (in press). Argos quality locations were provided from the KiwiSat 101 and SMRU solar satellite tags. The Sirtrack GPS-Argos and SMRU GPS-GSM tags provided Fastloc GPS locations. The GPS-GSM tag relayed data via mobile phone receivers. All the other tags relayed data via the Argos satellite system. General foraging location indicated with ‘Greece’ means those that had foraging locations in Greece excluding Zakynthos.

turtle id	tag type	date attached	duration of tracking (days)	M/F	beach/sea	foraging location
A	KiwiSat 101	27/6/2004	130	F	beach	Adriatic
B	KiwiSat 101	28/6/2004	279	F	beach	Adriatic
C	KiwiSat 101	29/6/2004	760	F	beach	North Africa
D	KiwiSat 101	16/6/2005	189	F	beach	Adriatic
E	KiwiSat 101	19/6/2005	419	F	beach	Adriatic
F	KiwiSat 101	21/6/2005	392	F	beach	Adriatic
G	KiwiSat 101	10/8/2005	118	F	beach	North Africa
4594	KiwiSat 101	7/5/2007	128	M	sea	Turkey
15119_07	Sirtrack GPS-Argos	10/5/2007	51	M	sea	Adriatic
Sotiris	Sirtrack GPS-Argos	8/5/2007	49	M	sea	Zakynthos
15119_08	Sirtrack GPS-Argos	3/5/2008	368	M	sea	Adriatic
15120	Sirtrack GPS-Argos	4/5/2008	315	M	sea	Zakynthos
4395	Sirtrack GPS-Argos	3/5/2008	356	M	sea	Greece
61810	Sirtrack GPS-Argos	3/5/2009	103	M	sea	Adriatic
61813	Sirtrack GPS-Argos	2/5/2009	104	M	sea	Adriatic
TT1	SMRU GPS-GSM	2/5/2009	246	F	sea	Adriatic
F_Solar	SMRU Solar	8/5/2009	145	F	sea	Greece

2. METHODS

2.1. Adult tracking

The Greek island of Zakynthos hosts the largest breeding population of loggerhead turtles (*Caretta caretta*) in the Mediterranean. The nesting beaches are situated around Laganas Bay in the southeastern part of the island (37°43' N, 20°52' E). During May 2007–2009, we attached transmitters to adult male ($n=8$) and female ($n=2$) loggerhead turtles captured at sea within 1 km of shore in the vicinity of the nesting beaches (for capture methodology, see Schofield *et al.* in press). This is just prior to the start of the nesting season and a time when males and females aggregate for mating. Details of tags are given in table 1. Units provided either GPS quality locations and/or Argos quality locations relayed either via the Argos satellite system or via mobile phone networks. We also digitized the previously published tracks (Zbinden *et al.* 2008) for female loggerhead turtles satellite tagged ($n=7$) on the nesting beaches at Zakynthos.

The data were filtered using a maximum rate of travel of 5 km h⁻¹ between successive locations. Foraging sites used at the end of post-breeding movements were identified by individuals slowing down and staying in approximately (all filtered locations within 30 km) the same place for more than 5 days. Lengthening this period from 5 to, for example, 15 days makes no difference to the definition of the foraging sites. We selected 5 days so that we could include datasets for adults where the satellite tags failed shortly after arrival at the foraging sites. Foraging sites were identified in essentially the same way by Zbinden *et al.* (2008), i.e. turtles remaining in fixed areas for extended periods.

2.2. Particle tracking

A state-of-the-art hydrodynamic model of the Mediterranean Sea (Bozec *et al.* 2006, 2008) was coupled with a

particle tracking algorithm (Mariani *et al.* in press) to simulate dispersion patterns of numerical drifters initially released in the upper layers (less than 6 m) of a small region (45 × 45 km) centred *ca* 40 km south of the nesting beaches of Zakynthos island. The physical ocean model is an eddy permitting configuration of OPA (Océan Parallélisé; Madec *et al.* 1998) in the Mediterranean Sea and it has a 1/8° of horizontal resolution and 43 layers in the vertical. The model has been successfully applied to study water mass formation in the Mediterranean (Bozec *et al.* 2008) and major patterns of the surface and deep thermohaline circulation of the eastern basin (Beranger *et al.* 2004; Bozec *et al.* 2006). Velocity data are extracted from the archived hydrodynamic simulations and linearly interpolated to the particle positions that are then integrated forward in time using a Runge–Kutta second-order scheme. A similar Lagrangian method was applied to reproduce dispersion patterns of fish larvae in the northwest Mediterranean and the model was used to simulate retention and dispersion processes of bluefin tuna larvae around the Balearic Islands (Mariani *et al.* in press).

The model was run for four separate years: 1998–2001. These are years in which high-resolution atmospheric forcing data (ECMWF, 0.5 × 0.5°) allow a good representation of the oceanic circulation and of air–sea exchanges (Bozec *et al.* 2008). Moreover, those years (1998–2001) cover a large range of surface conditions in the central Mediterranean and so provide a good indication of the extent of interannual variability in particle dispersion in the area (Bozec *et al.* 2008).

The nesting season at Zakynthos peaks in the second half of June and throughout July with the peak hatchling season extending through August and September (Margaritoulis 2005). To simulate hatchlings entering the water, passive and neutrally buoyant numerical particles were released every 5 days from the start of

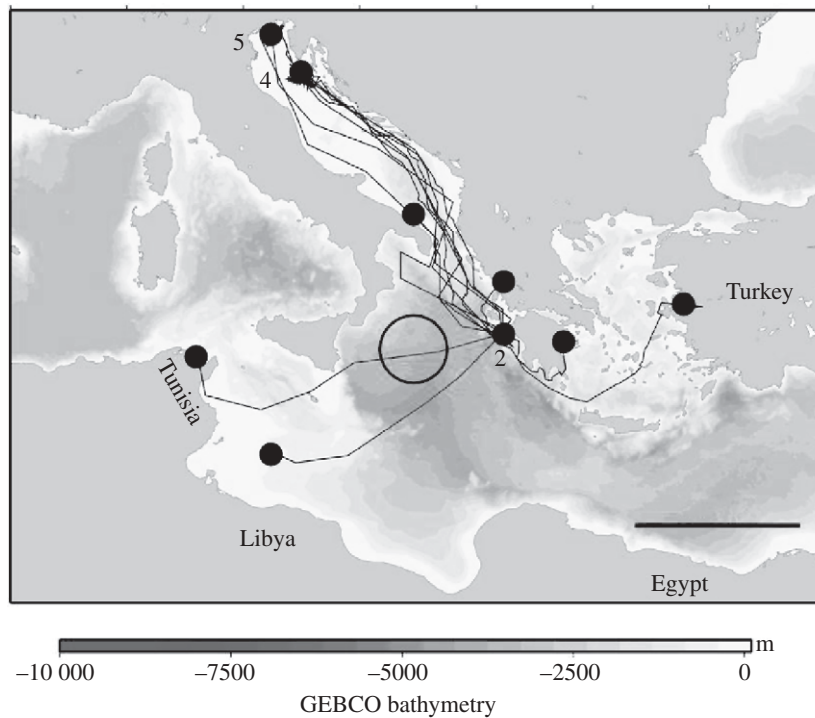


Figure 1. The post-breeding tracks of 17 adult loggerhead turtles tracked from Zakynthos. Tracks radiate out from Zakynthos in the Ionian Sea. Tracks heading north enter the Adriatic. Tracks heading southwest end up off Tunisia and Libya. The location of foraging areas is indicated by the black circles. Large open circle indicates approximate overwintering location for two turtles that headed south out of the Adriatic at the end of the summer. Numbers next to each foraging area indicate the number of turtles tracked to that foraging area (if no number then only one turtle travelled to that foraging area). Scale bar, 500 km.

August to the end of September and for four consecutive years 1998–2001 (total 288 000 particles and 48 releases). In each release, the drifting period was 180 days and, along their trajectories, particles are constrained in the upper 6 m of the water column. Without data assimilation, the model is unable to entirely reproduce observed wind-driven mesoscale features and over time it is likely that any errors in the particles' trajectories accumulate. Hence, we constrained the model to 180-day simulations. The numerical integration was performed using a time step of 60 s, while the positions of the particles were stored every day.

2.3. Drifter data

To assess the long-term drift scenarios, we used the Global Lagrangian Drifter Data freely available from <http://www.aoml.noaa.gov/envids/>. This dataset consists of satellite-tracked buoys drogued near the surface (15 m) from 1979 to the present. Drifter locations are estimated from 16 to 20 satellite fixes per day, per drifter. The Drifter Data Assembly Center (DAC) at NOAA's Atlantic Oceanographic and Meteorological Laboratory (AOML) assembles these raw data, applies quality control procedures and interpolates them via kriging to regular 6-h intervals.

To describe the drifter-inferred circulation in the Adriatic, we used drifter tracks published in Falco *et al.* (2000) that are not in the AOML database. For the eastern Mediterranean we used current patterns described in Hamad *et al.* (2006).

3. RESULTS

3.1. Adult tracking

A total of 17 loggerhead turtles were followed to their foraging grounds (figure 1). Foraging grounds were widely scattered across the Mediterranean: 10 individuals (59%) travelled north to foraging sites in the Adriatic, two travelled southwest to Tunisia and eastern Libya, two remained at Zakynthos close (within 10 km) to the breeding beaches, two travelled to other coastal sites in Greece and one travelled to Turkey. Two of the turtles that travelled to the northern Adriatic subsequently overwintered just south of Italy, but for clarity these components of the tracks are not shown.

3.2. Particle tracking

Particles showed a broad pattern of dispersion from Zakynthos, with a general dichotomy between northerly and southerly drift scenarios (figure 2). As well as this general pattern of dispersion, there were clear interannual and seasonal differences, with both year and week of release significantly affecting the percentage of particles ending up north of Zakynthos (two-way analysis of variance, for year: $F_{3,33} = 19.4$, $p < 0.001$; for week: $F_{11,33} = 4.7$, $p < 0.01$). For example, more particles ended up north of Zakynthos when released in 2000 (94%) compared with 1999 (53%), and when released in the last week of September (94%) compared with the first week of August (41%) (figure 3).

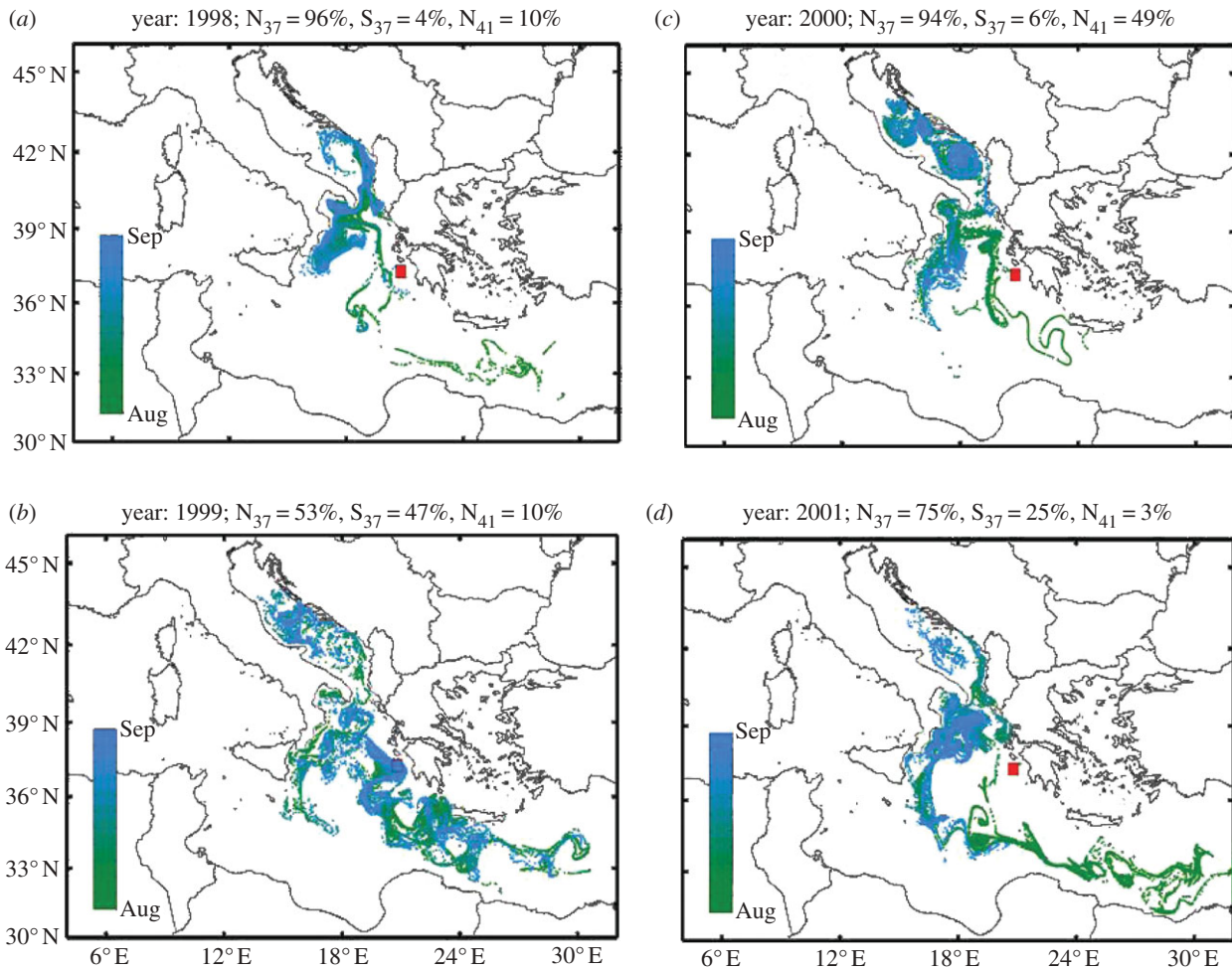


Figure 2. Particle-tracking results for different years. Each plot shows the endpoint (after 180 days) of 6000 particles released at 5-day intervals during August and September (12 release dates in all). For each year, the percentage of particles ending up north and south of 37° N after 180 days is shown (N_{37} and S_{37} , respectively), as well as the percentage ending up north of 41° N (i.e. the southern Adriatic) (N_{41}). Colour code denotes the release date grading from green (start of August) to blue (end of September). The area of initial particle release is shown in red.

3.3. Drifter trajectories

The AOML satellite-tracked drifters allow us to extend the results from the particle tracking model. Buoys travelling through the area between Zakynthos and southern Sicily (i.e. in the Ionian Sea) could travel southwards to the North Africa coast, and from there other buoys have been tracked travelling westwards to Tunisia and eastern Libya. So, it is possible for passive drift to occur from Zakynthos to Tunisia and eastern Libya in approximately 1–2 years (figure 4). Satellite-tracked drifter trajectories reveal a very consistent circulation in the Adriatic with currents flowing northwards in the eastern Adriatic and southwards in the western Adriatic. Therefore, it is possible to end up by passive drift in the northern Adriatic in less than 1 year. In the eastern Mediterranean, strong eddies superimpose on a general cyclonic (anticlockwise) circulation, explaining how particles may passively end up in the Aegean Sea from Zakynthos. We can therefore combine the results from the particle tracking, AOML drifter trajectories and wider oceanography to schematically illustrate the various drift scenarios for hatchlings from Zakynthos (figure 5).

4. DISCUSSION

It is clear that adult loggerhead turtles breeding at Zakynthos disperse widely through the Mediterranean, heading broadly north, south and east. Our satellite-tracking records corroborate findings from conventional flipper tagging, albeit with the caveat of potentially selective reporting of flipper tags (Margaritoulis *et al.* 2003). Our findings contrast with those from some other rookeries. For example, large numbers of leatherback turtles (*Dermochelys coriacea*) breeding on the Indian Ocean beaches of South Africa have been satellite-tracked and all travel consistently southwards to foraging grounds in the Agulhas and Benguela currents (Lambardi *et al.* 2008). Similarly, large numbers of green turtles (*Chelonia mydas*) have been satellite-tracked from breeding beaches at Ascension Island in the mid-Atlantic, and all head subsequently to foraging sites on the coast of South America following similar routes (Papi *et al.* 2000). Certainly, after the breeding season, adult loggerhead turtles are not simply passively transported by currents to their feeding grounds, since they are strong swimmers and individuals maintain very tight fidelity to specific foraging

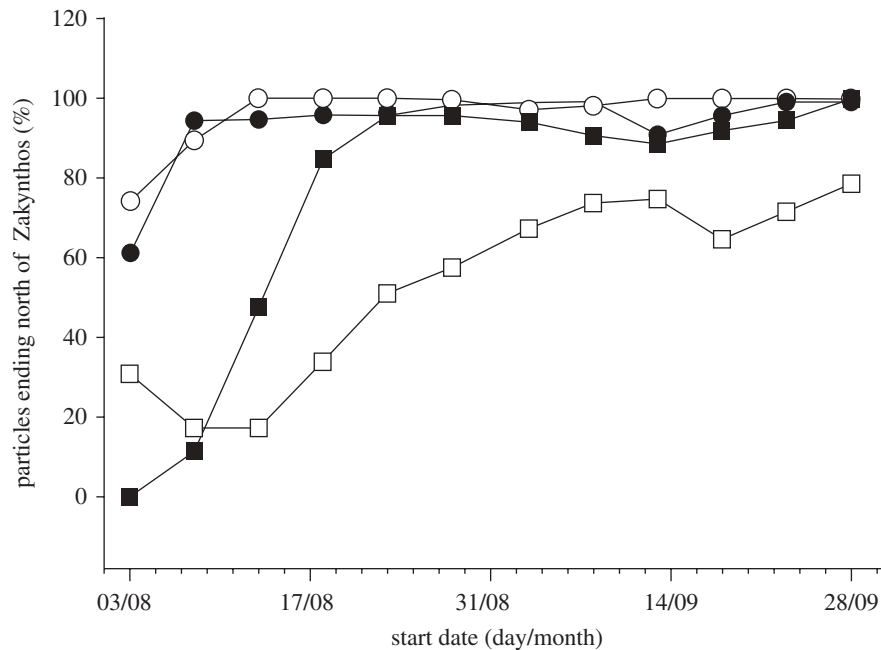


Figure 3. Interannual and seasonal variability in the percentage of particles ending up north of Zakynthos (endpoint more than 37° N), 180 days after start dates in August and September. Open circles, 1998; open squares, 1999; filled circles, 2000; filled squares, 2001. Particles had a greater tendency to end up north when released in September compared with August, and in 1998, 2000 and 2001 compared with 1999.

sites (Broderick *et al.* 2007). However, we propose that current patterns do influence adult post-breeding migrations through another mechanism: namely that adult post-breeding migration destinations are linked to hatchling drift patterns. According to this hypothesis we predicted a wide range of drift patterns from Zakynthos and found evidence for this pattern. Our methodology of inferring hatchling drift patterns raises a number of questions.

How likely do the drifter trajectories and modelled currents reflect hatchling turtle drift scenarios? We first assumed that hatchlings started drifting, when offshore, from breeding beaches on Zakynthos. Upon entering the sea, hatchling turtles show a short period of intense offshore-directed swimming known as the swimming frenzy. This behaviour is thought to last from a few hours to a few days and transport hatchlings up to a few tens of kilometres offshore (Salmon & Wyneken 1987). After the swimming frenzy, hatchlings are thought to drift passively (Carr & Meylan 1980). Hence, our assumption of passive drift from a site close offshore seems reasonable. The semi-enclosed Laganas Bay and its nesting beaches face southwards, and so we selected an area for particle release south of the island. It would, however, be interesting to investigate how changes in the release point impact the subsequent trajectories. In some areas where there are large changes in the current patterns over small scales, for example in the Gulf Stream off Florida, small changes in the release point would presumably impact the drift scenario appreciably. As hatchlings grow into juvenile turtles and their swimming ability improves, it has been hypothesized that they might show directional swimming to help stay in broadly favourable areas (Lohmann *et al.* 2001). However, after 2 years, the estimated size of

loggerhead turtles is still only about 20 cm carapace length (Hays & Marsh 1997), and so in their first years of life, the assumption of passive drift of varying degrees, depending on season and location, is probably valid. Assuming passive drift is one thing, but how accurately can we estimate drift patterns?

The oceanography of the Mediterranean is now well established through intensive targeted programmes that mainly use satellite-tracked drifters and particle-tracking models to estimate surface currents. It would be useful to match years for the particle-tracking simulations with the drifter data. However, this was not possible as there was limited drifter data available and the particle-tracking model was limited to years when surface currents have been validated (Bozec *et al.* 2008). Nevertheless, matching the different current datasets to the same years and examining the extent of interannual variability in currents over more extended periods would certainly be useful. The advantage of drifters is that they show ‘real’ patterns of drift. Their limitation is that in areas of interest there may be relatively few drifter trajectories or the data may not be publicly available. Hence, particle-tracking models have been developed which allow the ocean to be seeded with huge numbers of particles that are then advected in a modelled ocean that is forced by realistic physical data (Bozec *et al.* 2006). The advantage of these models is that they allow a large number of trajectories to be examined and more specific questions about spatio-temporal variability in currents to be explored. The model we used here appears to reproduce well the major surface and deeper circulation patterns in the eastern Mediterranean (Beranger *et al.* 2004; Bozec *et al.* 2006, 2008; Mariani *et al.* in press). In addition, the resolution of the model allows it to simulate the

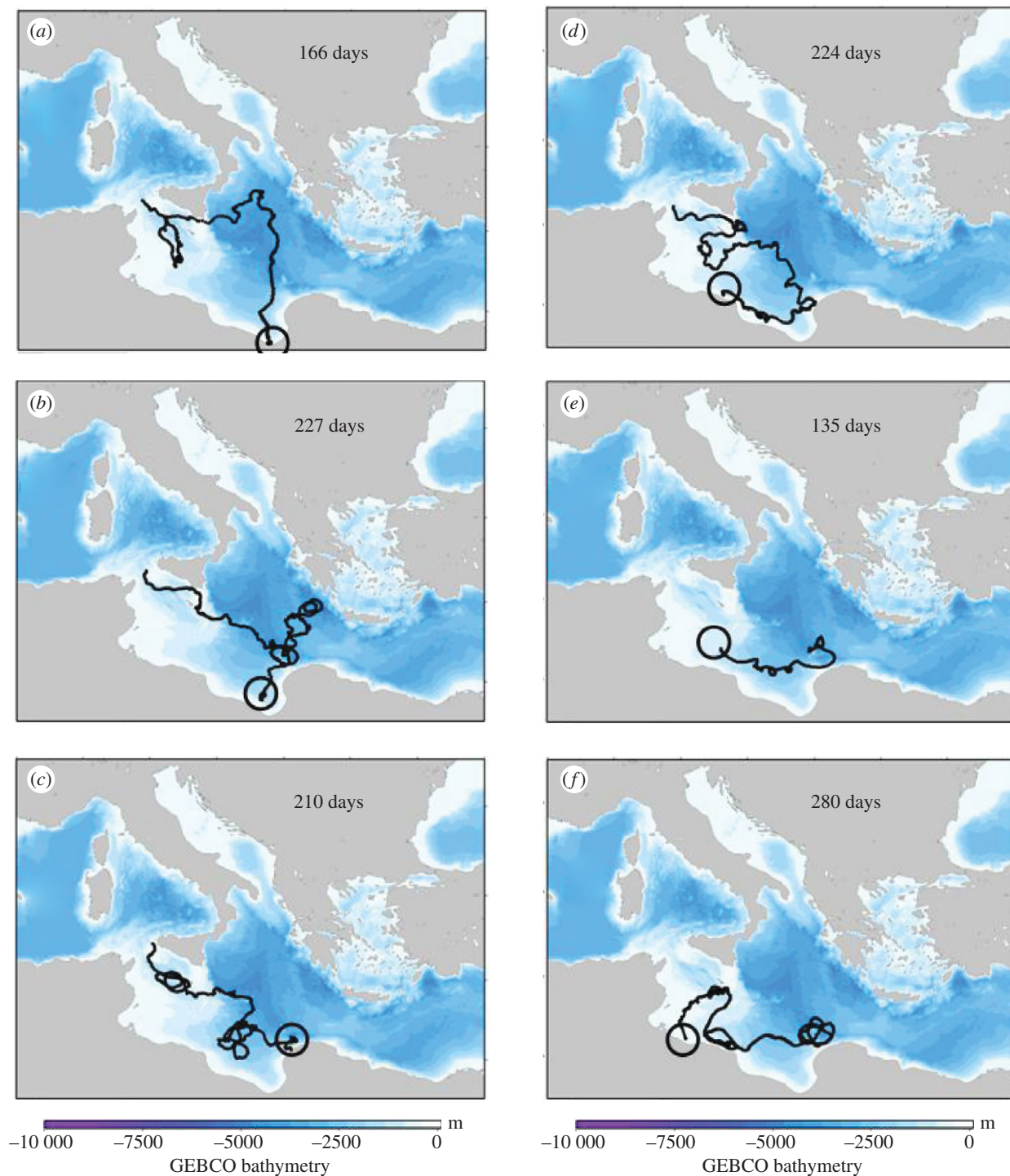


Figure 4. Trajectories of satellite-tracked drifters. Circles indicate endpoint of each trajectory. The duration of each track is indicated in each panel. Buoys are selected to indicate possible drift scenarios from Zakynthos to Tunisia and eastern Libya. Panels (a–c) show buoy drift to North Africa from points in the central Mediterranean attained by particles within 180 days of leaving Zakynthos. Panels (d–f) indicate how the drift to North Africa might then continue with westward movement towards Tunisia.

effects of mesoscale dynamics in this area and hence provides a realistic prediction of real drift patterns. The Ionian basin is notably characterized by a seasonal and interannual variability of the Atlantic Ionian Stream (AIS, i.e. a branch of the modified Atlantic water flow), and by several active circulation features in the central and eastern part of the basin (Beranger *et al.* 2005; Hamad *et al.* 2006). In August and September, the model's simulations revealed that close to

Zakynthos there is a bifurcation of the current with northward and southward flowing branches. In short, we would therefore predict that some hatchlings will get advected broadly north to the Adriatic Sea and others will get advected broadly south from Zakynthos. Interestingly, the local circulation pattern changes between August and September (Pinardi & Masetti 2000; Hamad *et al.* 2006; Gerin *et al.* 2009), resulting in a seasonal change in the probability of north versus

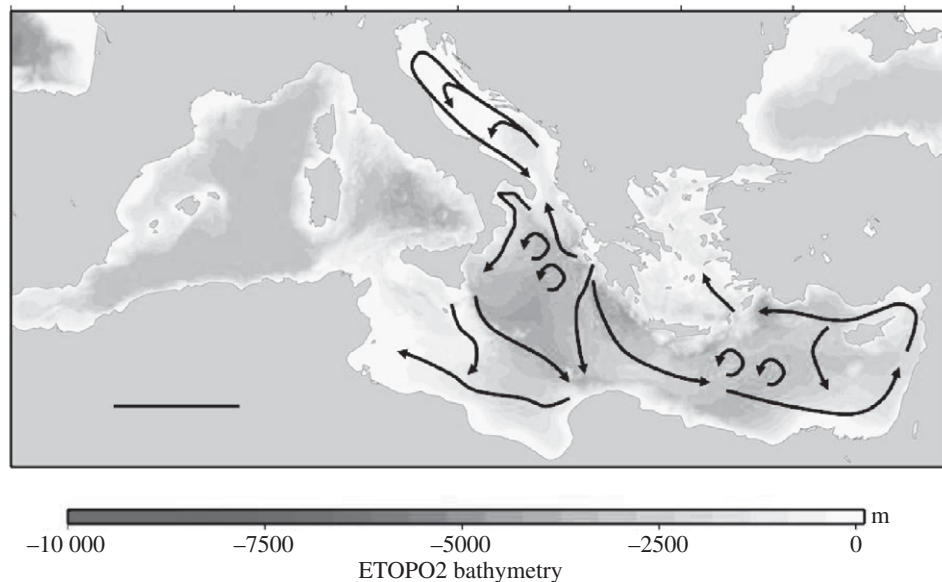


Figure 5. Schematic illustration of likely drift patterns for hatchling turtles from Zakynthos. The scheme is produced by blending the results from the particle-tracking model (figure 2), AOML drifter trajectories (figure 4), previously published drifter trajectories for the Adriatic (Falco *et al.* 2000) and the oceanography of the eastern Mediterranean derived from a mix of satellite and hydrodynamic datasets (Hamad *et al.* 2006). Scale bar, 500 km.

south advection. This implies that depending on when they emerge during the season, hatchlings will have different drift trajectories.

This finding poses interesting implications for climate change and sea turtles. First, sea turtles exhibit temperature-dependent sex determination with males being produced at cooler incubation temperatures. If male and female hatchlings emerge at different times of the season, then our results suggest that they may have different drift scenarios that might lead to male/female differences in adult migration routes. However, to date, very few male turtles have been tracked so that it is difficult to test this idea. Increased sample sizes may also reveal whether there are sex differences in foraging location. Second, it has been hypothesized that climate change may cause ocean currents to shift (Poloczanska *et al.* 2009), and this in turn might give rise to new post-breeding adult migrations.

After their initial northward and southward drifts, we can use Lagrangian drifter trajectories and information on the general surface circulation of the Mediterranean to infer the long-term (more than 180 days) drift scenarios for hatchlings. For example, the Adriatic Sea has a very well-established circulation with a current flowing northwards in the eastern Adriatic before turning and flowing south in the western Adriatic (Falco *et al.* 2000; Poulain 2001). South of Zakynthos the Ionian Surface Water (ISW; Malanotte-Rizzoli *et al.* 1997) currents flow southeastwards towards the northeast coast of Libya, and the northwest coast of Egypt, from where some drifters travel westwards towards Tunisia. Hatchlings entering the eastern Mediterranean would be expected to disperse widely in the complex circulation characterized by strong eddies in the general cyclonic circulation along the coast of Egypt, Syria and Turkey (e.g. Hamad *et al.* 2006). Hence, hatchlings initially carried south would then have a broad range of drift scenarios across the eastern

Mediterranean and North Africa. Our satellite-tracking results, and those of others, identified the coast of Tunisia as an important foraging site for sea turtles (Zbinden *et al.* 2008). Yet, it is clear from our particle-tracking results that hatchlings would not travel directly to that site. Instead, it can be hypothesized that arrival on the coast of Tunisia and eastern Libya would follow a more extended (more than 180 days) Mediterranean drift. Also of interest in the particle-tracking results is the finding that after 180 days, some particles may still be very close to Zakynthos. We found that some adult turtles remained at Zakynthos after the end of the breeding season. It may be that these are individuals that did not disperse far from the island as hatchlings and juveniles.

While we predict strong linkages between the extent of hatchling dispersal and adult post-breeding migrations, on the broadest scale clearly not all hatchling drift patterns will generate possible scenarios for adult migration. For example, some hatchlings may be carried into areas where they die because of environmental conditions. For example, in the Atlantic, a small number of loggerhead turtle hatchlings are carried on the Gulf Stream from nesting beaches in Florida to northern Europe where they die from cold (Hays & Marsh 1997). Hence, the adult post-breeding migrations may reflect a subset of successful hatchling drift scenarios.

We suggest that selection of a permanent foraging site may be influenced by the broad geographic area that individuals previously encountered in the pelagic drift phase. Clearly, over the course of several years juveniles will have the capacity to drift or actively swim to a huge range of locations throughout the Mediterranean and possibly beyond (Eckert *et al.* 2008; Kobayashi *et al.* 2008). However, the similarity between adult post-breeding tracks and inferred hatchling dispersion patterns suggests that it may be during this initial first year or so of hatchling dispersion that

individuals imprint on possible future and predictable foraging sites. During this time juveniles may experience many different sites and then as adults they may make a decision to go to the preferred one based on that experience, what we might term the ‘many targets experienced, one preferred’ hypothesis. Certainly, it has been suggested that hatchlings imprint on their nesting beach during their early days of life and maintain a memory of the nesting site (e.g. through the use of the site’s geomagnetic coordinates; Lohmann *et al.* 2008a). Similarly, imprinting on breeding locations occurs early in life in other groups such as migrating salmon (Quinn & Dittman 1992). Hence, it seems reasonable to hypothesize that sea turtles imprint on potential predictable foraging sites during their early life.

While we recorded broad dispersion of adults, it is clear that the Adriatic Sea is an important foraging site for loggerhead turtles from Greece. Meta-analysis of the tracks of larger numbers of adult loggerhead turtles might allow more precise estimates of the proportion of this breeding population that travels to different areas of the Mediterranean, but it appears that the high proportion of adults foraging in the Adriatic Sea reflects a large proportion of hatchlings being advected there from Zakynthos.

Our results support the hypothesis that adult dispersion patterns after breeding may reflect their previous drift scenarios as hatchlings. To test this hypothesis further it may be possible to extend and refine the type of analysis performed here to a range of other turtle rookeries around the world. Given the plethora of adult-tracking studies (e.g. Lohmann *et al.* 2008b) as well as the wide availability of both drifter trajectories and complementary particle-tracking models, such meta-analysis should be possible.

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REFERENCES

- Alerstam, A. 2006 Conflicting evidence about long-distance animal navigation. *Science* **313**, 791–794. (doi:10.1126/science.1129048)
- Alerstam, T., Hedenstrom, A. & Akesson, S. 2003 Long-distance migration: evolution and determinants. *Oikos* **103**, 247–260. (doi:10.1034/j.1600-0706.2003.12559.x)
- Beranger, K., Mortier, L., Gasparini, G. P., Gervasio, L., Astraldi, M. & Crepon, M. 2004 The dynamics of the Sicily Strait: a comprehensive study from observations and models. *Deep-Sea Res. II* **51**, 411–440. (doi:10.1016/j.dsr2.2003.08.004)
- Beranger, K., Mortier, L. & Crepon, M. 2005 Seasonal variability of water transport through the Straits of Gibraltar, Sicily and Corsica, derived from a high-resolution model of the Mediterranean circulation. *Prog. Oceanogr.* **66**, 341–364. (doi:10.1016/j.pocean.2004.07.013)
- Bolten, A. B., Martins, H. R., Bjorndal, K. A., Cocco, M. & Gerosa, G. 1992 *Caretta caretta* (loggerhead). Pelagic movement and growth. *Herpetol. Rev.* **23**, 116.
- Bozec, A., Bouruet-Aubertot, P., Beranger, K. & Crepon, M. 2006 Mediterranean oceanic response to the interannual variability of a high-resolution atmospheric forcing: a focus on the Aegean Sea. *J. Geophys. Res. Oceans* **111**, C11013. (doi:10.1029/2005JC003427)
- Bozec, A., Bouruet-Aubertot, P., Iudicone, D. & Crepon, M. 2008 Impact of penetrative solar radiation on the diagnosis of water mass transformation in the Mediterranean Sea. *J. Geophys. Res. Oceans* **113**, C06012. (doi:10.1029/2007JC004606)
- Broderick, A. C., Coyne, M. S., Fuller, W. J., Glen, F. & Godley, B. J. 2007 Fidelity and over-wintering of sea turtles. *Proc. R. Soc. B* **274**, 1533–1538. (doi:10.1098/rspb.2007.0211)
- Carr, A. & Meylan, A. B. 1980 Evidence of passive migration of green turtle hatchlings in Sargassum. *Copeia* **1980**, 366–368. (doi:10.2307/1444022)
- Chapman, J. W., Reynolds, D. R., Mouritsen, H., Hill, J. K., Riley, J. R., Sivell, D., Smith, A. D. & Woivod, I. P. 2008a Wind selection and drift compensation optimize migratory pathways in a high-flying moth. *Curr. Biol.* **18**, 514–518. (doi:10.1016/j.cub.2008.02.080)
- Chapman, J. W., Reynolds, D. R., Hill, J. K., Sivell, D., Smith, A. D. & Woivod, I. P. 2008b A seasonal switch in compass orientation in a high-flying migratory moth. *Curr. Biol.* **18**, R908–R909. (doi:10.1016/j.cub.2008.08.014)
- Darwin, C. 1873 Perception in the lower animals. *Nature* **7**, 360. (doi:10.1038/007360c0)
- Dingle, H. & Drake, V. A. 2007 What is migration? *Bioscience* **57**, 113–121. (doi:10.1641/B570206)
- Eckert, S. A., Moore, J. E., Dunn, D. C., van Buiten, R. S., Eckert, K. L. & Halpin, P. N. 2008 Modelling loggerhead turtle movement in the Mediterranean: importance of body size and oceanography. *Ecol. Appl.* **18**, 290–308. (doi:10.1890/06-2107.1)
- Falco, P., Griffa, A., Poulain, P.-M. & Zambianchi, E. 2000 Transport properties in the Adriatic Sea as deduced from drifter data. *J. Phys. Oceanogr.* **30**, 2055–2071. (doi:10.1175/1520-0485(2000)030<2055:TPITAS>2.0.CO;2)
- Galef Jr, B. G. & Laland, K. N. 2005 Social learning in animals: empirical studies and theoretical models. *BioScience* **55**, 489–499. (doi:10.1641/0006-3568(2005)055[0489:SLIAES]2.0.CO;2)
- Gerin, R., Poulain, P.-M., Taupier-Letage, I., Millot, C., Ben Ismail, S. & Sammari, C. 2009 Surface circulation in the Eastern Mediterranean using drifters (2005–2007). *Ocean Sci.* **5**, 559–574.
- Hamad, N., Millot, C. & Taupier-Letage, I. 2006 The surface circulation in the eastern basin of the Mediterranean Sea. *Scientia Marina* **70**, 457–503.
- Hays, G. C. & 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)
- Kobayashi, D. R., Polovina, J. J., Parker, D. M., Kamezaki, N., Cheng, I. J., Uchida, I., Dutton, P. H. & Balazs, G. H. 2008 Pelagic habitat characterization of loggerhead sea

- turtles, *Caretta caretta*, in the North Pacific Ocean (1997–2006): insights from satellite tag tracking and remotely sensed data. *J. Exp. Mar. Biol. Ecol.* **356**, 96–114. (doi:10.1016/j.jembe.2007.12.019)
- Lambardi, P., Lutjeharms, J. R. E., Mencacci, R., Hays, G. C. & Luschi, P. 2008 Influence of ocean currents on long-distance movement of leatherback sea turtles in the South-west Indian Ocean. *Mar. Ecol. Prog. Ser.* **353**, 289–301. (doi:10.3354/meps07118)
- Lee, P. L. M. 2008 Molecular ecology of marine turtles: new approaches and future directions. *J. Exp. Mar. Biol. Ecol.* **356**, 25–42. (doi:10.1016/j.jembe.2007.12.021)
- Lohmann, K. J., Cain, S. D., Dodge, S. A. & Lohmann, C. M. F. 2001 Regional magnetic fields as navigational markers for sea turtles. *Science* **294**, 364–366. (doi:10.1126/science.1064557)
- Lohmann, K. J., Putman, N. F. & Lohmann, C. M. F. 2008a Geomagnetic imprinting: a unifying hypothesis of long-distance natal homing in salmon and sea turtles. *Proc. Natl Acad. Sci. USA* **105**, 19 096–19 101. (doi:10.1073/pnas.0801859105)
- Lohmann, K. J., Luschi, P. & Hays, G. C. 2008b Goal navigation and island-finding in sea turtles. *J. Exp. Mar. Biol. Ecol.* **356**, 83–95. (doi:10.1016/j.jembe.2007.12.017)
- Luschi, P., Hays, G. C. & Papi, F. 2003 A review of long-distance movements by marine turtles and the possible role of ocean currents. *Oikos* **103**, 293–302. (doi:10.1034/j.1600-0706.2003.12123.x)
- Madec, G., Delecluse, P., Imbard, M. & Lévy, C. 1998 OPA 8.1 Ocean General Circulation Model reference manual, 1–91. Paris, France: Institut Pierre-Simon Laplace.
- Malanotte-Rizzoli, P. et al. 1997 A synthesis of the Ionian Sea hydrography, circulation and water mass pathways during POEM Phase I. *Prog. Oceanogr.* **39**, 153–204. (doi:10.1016/S0079-6611(97)00013-X)
- Margaritoulis, D. 2005 Nesting activity and reproductive output of loggerhead sea turtles, *Caretta caretta*, over 19 seasons (1984–2002) at Laganas Bay, Zakynthos, Greece: the largest rookery in the Mediterranean. *Chel. Cons. Biol.* **4**, 916–929.
- Margaritoulis, D. et al. 2003 Loggerhead turtles in the Mediterranean Sea: present knowledge and conservation perspectives. In *Loggerhead sea turtles* (eds A. B. Bolten & B. Witherington), pp. 175–198. Washington, DC: Smithsonian Institution Press.
- Mariani, P., MacKenzie, B. R., Iudicone, D. & Bozec, A. In press. Modelling retention and dispersion mechanisms of bluefin tuna eggs and larvae in the Northwest Mediterranean Sea. *Prog. Oceanogr.*
- Papi, F., Luschi, P., Åkesson, S., Capogrossi, S. & Hays, G. C. 2000 Open-sea migration of magnetically disturbed sea turtles. *J. Exp. Biol.* **203**, 3435–3443.
- Perdeck, A. C. 1958 Two types of orientation in migrating starlings, *Sturnus vulgaris* L., and chaffinches, *Fringilla coelebs* L., as revealed by displacement experiments. *Ardea* **46**, 1–37.
- Pinardi, N. & Masetti, E. 2000 Variability of the large scale general circulation of the Mediterranean Sea from observations and modelling: a review. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **158**, 153–174. (doi:10.1016/S0031-0182(00)00048-1)
- Poloczanska, E. S., Limpus, C. J. & Hays, G. C. 2009 Vulnerability of marine turtles to climate change. *Adv. Mar. Biol.* **56**, 151–211. (doi:10.1016/S0065-2881(09)56002-6)
- Poulain, P. M. 2001 Adriatic Sea surface circulation as derived from drifter data between 1990 and 1999. *J. Mar. Sys.* **29**, 3–32. (doi:10.1016/S0924-7963(01)00007-0)
- Quinn, T. P. & Dittman, A. H. 1992 Fishes. In *Animal homing* (ed. F. Papi), pp. 145–211. London, UK: Chapman & Hall.
- Salmon, M. & Wyneken, J. 1987 Orientation and swimming behaviour of hatchling loggerhead turtles *Caretta caretta* L. during their offshore migration. *J. Exp. Mar. Biol. Ecol.* **109**, 137–153. (doi:10.1016/0022-0981(87)90012-8)
- Schofield, G., Lilley, M. K. S., Bishop, C. M., Brown, P., Katselidis, K. A., Dimopoulos, P., Pantis, J. D. & Hays, G. C. In press. Conservation hotspots: implications of intense spatial area use by breeding male and female loggerheads at the Mediterranean's largest rookery. *Endang. Species Res.* (doi:10.3354/esr00137)
- Sims, D. W., Southall, E. J., Richardson, A. J., Reid, P. C. & Metcalfe, J. D. 2003 Seasonal movements and behaviour of basking sharks from archival tagging: no evidence of winter hibernation. *Mar. Ecol. Prog. Ser.* **248**, 187–196. (doi:10.3354/meps248187)
- Zbinden, J. A., Aebischer, A., Margaritoulis, D. & Arlettaz, D. 2008 Important areas at sea for adult loggerhead sea turtles in the Mediterranean Sea: satellite tracking corroborates findings from potentially biased sources. *Mar. Biol.* **153**, 899–906. (doi:10.1007/s00227-007-0862-2)