The Company of Biologists

REVIEW

There and back again: natal homing by magnetic navigation in sea turtles and salmon

Kenneth J. Lohmann* and Catherine M. F. Lohmann

ABSTRACT

Diverse marine animals migrate across vast expanses of seemingly featureless ocean before returning as adults to reproduce in the area where they originated. How animals accomplish such feats of natal homing is an enduring mystery. Growing evidence suggests, however, that sea turtles and salmon imprint on the magnetic field of their home area when young and then use this information to return as adults. Both turtles and salmon have the sensory abilities needed to detect the unique 'magnetic signature' of a coastal area. Analyses have revealed that, for both groups of animals, subtle changes in the geomagnetic field of the home region are correlated with changes in natal homing behavior. In turtles, a relationship between population genetic structure and the magnetic fields that exist at nesting beaches has also been detected, consistent with the hypothesis that turtles recognize their natal areas on the basis of magnetic cues. Salmon likely use a biphasic navigational strategy in which magnetic cues guide fish through the open sea and into the proximity of the home river where chemical cues allow completion of the spawning migration. Similarly, turtles may also exploit local cues to help pinpoint nesting areas once they have arrived in the vicinity. Throughout most of the natal homing migration, however, magnetic navigation appears to be the primary mode of long-distance guidance in both sea turtles and salmon.

KEY WORDS: Magnetoreception, Migration, Geomagnetic imprinting, Orientation, Philopatry

Introduction

Natal homing refers to a pattern of behavior in which animals leave their geographic area of origin when young, migrate considerable distances, and then return to the area of origin to reproduce (Meylan et al., 1990; Lohmann et al., 2008a; Rooker et al., 2008). Diverse animals exhibit natal homing, including some fishes (Rooker et al., 2008; Feldheim et al., 2014), reptiles (Meylan et al., 1990; Bowen et al., 2004; Lohmann et al., 2013), birds (Wheelwright and Mauck, 1998; Welch et al., 2012) and mammals (Baker et al., 2013). Until recently, however, little was known about how long-distance natal homing is accomplished by any animal.

Sea turtles and salmon are iconic long-distance ocean migrants with extraordinary navigational abilities. Many species and populations exhibit natal homing (Groot and Margolis, 1991; van Buskirk and Crowder, 1994; Quinn, 2005). Salmon are known to exploit chemical cues to identify their home streams at the end of spawning migrations (Hasler and Scholz, 1983; Dittman and Quinn, 1996), and turtles have similarly been hypothesized to use chemical cues as they complete reproductive migrations (Grassman et al.,

Department of Biology, University of North Carolina, Chapel Hill, NC 27599, USA.

*Author for correspondence (KLohmann@email.unc.edu)

K.J.L., 0000-0003-1068-148X; C.M.F.L., 0000-0003-3767-0967

1984; Lohmann et al., 2008b; Endres et al., 2016). Such cues do not, however, extend far enough into the ocean to guide migrations that begin at widely separated geographic locations and can span more than a thousand kilometers of open sea (Lohmann et al., 2013). Thus, how salmon and turtles navigate across vast expanses of ocean to arrive at a particular natal area has remained a mystery.

Much of a sea turtle's navigational repertoire depends upon its ability to detect Earth's magnetic field (Lohmann, 1991; Lohmann and Lohmann, 1996a, 2003; Luschi et al., 2007). Sea turtles are known to have both a magnetic compass sense, which enables them to determine their magnetic heading (Lohmann, 1991; Lohmann and Lohmann, 1993), and a magnetic map sense which enables them to assess geographic position (Lohmann et al., 2001, 2004, 2012; Putman et al., 2011). The map sense depends on an ability to differentiate among locations based on features of Earth's field that vary geographically. Turtles can, for example, distinguish between magnetic fields that exist at different locations along the southeastern US coast (Lohmann et al., 2004). Recent evidence implies that salmon have similar abilities (Putman et al., 2013, 2014a,b).

The use of magnetic navigation by sea turtles and salmon has led to the geomagnetic imprinting hypothesis of natal homing, which proposes that these animals imprint on the magnetic field of their home regions when young and use this information to return as adults (Lohmann et al., 1999, 2008a,b). In this Review, we first discuss natal homing and how animals might use the magnetic signature of a natal area to return to the proximity of a particular location. We then summarize the growing evidence that salmon and sea turtles do indeed use magnetic navigation to relocate their home areas during reproductive migrations. Finally, we consider the idea that animals learn the magnetic features of their natal areas when young and remember this information when they return to reproduce years later. Such learning has not yet been demonstrated empirically, but we discuss why current evidence is more compatible with the hypothesis of imprinting than with alternatives.

Migrations of sea turtles and salmon

Migratory salmon from many populations and species hatch in freshwater streams, enter the sea when young, and disperse hundreds or thousands of kilometers offshore before returning years later to their natal tributaries to spawn (Groot and Margolis, 1991; Quinn, 2005). This generalized description includes, but is not limited to, some populations of sockeye salmon (*Oncorhynchus nerka*), Chinook salmon (*Oncorhynchus tshawytscha*) and chum salmon (*Oncorhynchus keta*) found in the Pacific Northwest of the North American continent. Natal homing is often very precise in that fish frequently return to a river of origin and sometimes to a particular river branch (Quinn et al., 1999).

Most species of sea turtles leave their natal beaches as hatchlings, migrate to the open sea, and spend several years in distant oceanic and/or neritic areas before eventually returning to the natal region to

reproduce. In some species, such as loggerhead turtles (*Caretta caretta*), young turtles typically follow complex migratory pathways that lead across entire ocean basins and may take a decade or more to complete (Bjorndal et al., 2000; Mansfield and Putman, 2013). In other species, such as the Kemp's ridley turtle (*Lepidochelys kempii*) and the green turtle (*Chelonia mydas*), the duration of the oceanic phase may be shorter but turtles still travel hundreds or thousands of kilometers from their natal beaches (Lutz and Musick, 1997). Genetic analyses have suggested that the precision of natal homing varies considerably among different populations and species. Homing to regions of coastline several hundred kilometers in length is common, although reaching some targets requires greater precision, e.g. the 30 km stretch of beach used by Kemp's ridley turtles (Bowen and Avise, 1995; Bowen and Karl, 2007; Lohmann et al., 2008a; Putman and Lohmann, 2008).

Biphasic navigation

Growing evidence indicates that salmon and sea turtles probably accomplish natal homing in two distinct steps. The first involves long-distance movements through the open sea into the vicinity of the natal area and is likely guided by magnetic navigation and geomagnetic imprinting (Lohmann et al., 2008a,b; Putman et al., 2013; Brothers and Lohmann, 2015). The second involves localization of a suitable site for reproduction and, at least for salmon, is mediated by olfactory cues, olfactory imprinting and possibly pheromones (Nordeng, 1971; Hasler and Scholz, 1983; Groot et al., 1986; Dittman and Quinn, 1996). Indeed, navigational strategies that rely on different sensory cues that function over different spatial scales are probably typical for long-distance migrants (Lohmann et al., 2008b; Mouritsen, 2018).

Until less than a decade ago, all that was known for certain about natal homing was that salmon use chemical cues to identify their natal rivers or streams near the end of their spawning migration. That salmon imprint on the olfactory cues of their natal waterway has been demonstrated through experiments in which young fish were exposed to specific chemicals during a critical period of development and subsequently released to undergo their normal migrations; these artificially imprinted salmon returned as adults to breed in streams that had been scented with the same chemical (e.g. Hasler and Scholz, 1983; Dittman et al., 1996; Nevitt and Dittman, 1998). Given that turtles are able to detect both waterborne (Manton et al., 1972a,b) and airborne (Endres and Lohmann, 2012, 2013) chemical cues, it is plausible that turtles also use chemical cues in the final approach to their natal targets.

Under favorable conditions (for example, in fjords or other sheltered areas with limited vertical mixing), chemical cues from coastal areas might extend a considerable distance into the ocean (Lohmann et al., 2008b). However, chemical cues cannot extend across more than a thousand kilometers of ocean, the distance over which some populations of salmon and sea turtles routinely migrate (Dittman and Quinn, 1996; Lohmann et al., 1999). For this reason, navigation in the open sea has long been thought to involve mechanisms that are not olfactory (e.g. Hasler, 1971; Quinn, 2005; Lohmann et al., 1999, 2013).

The long-distance portion of the migration through the open sea can plausibly be explained by the known ability of sea turtles and salmon to exploit variations in Earth's magnetic field as a kind of magnetic positioning system or 'magnetic map' (Lohmann et al., 2004, 2007, 2012; Putman et al., 2013, 2014a,b). To explore how turtles, salmon and other marine animals might exploit magnetic navigation in natal homing, we will begin by highlighting several important features of Earth's magnetic field.

Earth's magnetic field

The geomagnetic field bears resemblance to the dipole field of a giant bar magnet in that field lines emerge from the southern hemisphere, curve around the planet, and re-enter the Earth in the northern hemisphere (Fig. 1). Several magnetic parameters vary across the surface of the globe. For example, the angle at which magnetic field lines intersect Earth's surface, known as the inclination angle, varies predictably with latitude. At the magnetic equator, field lines are parallel to Earth's surface and the inclination angle is 0 deg. Moving northward or southward from the equator, field lines become progressively steeper; at the magnetic poles themselves, field lines are perpendicular to Earth's surface and the inclination angle is 90 deg. The intensity (strength) of the magnetic field also varies geographically and in such a way that most locations in an ocean basin are marked by unique combinations of intensity and inclination (Lohmann et al., 2007).

Magnetic navigation: use of magnetic parameters in position finding

During most of the natal homing migration, the primary navigational challenge for sea turtles and salmon is to navigate across large expanses of open sea to a particular coastal area. Most major sea turtle rookeries, as well as the mouths of most major rivers where salmon spawn, are located along continental coastlines that are aligned approximately north to south (Lohmann et al., 2008a). Thus, the possibility exists that geomagnetic parameters can be used to identify specific coastal locations.

The coasts of North America illustrate the basic principle. Because the coastlines trend north–south while isoclinics (that is, isolines along which inclination angle is constant) trend east–west, every area of coastline is marked by a different inclination angle (Fig. 2A). Similarly, isodynamics (isolines of total field intensity) also run approximately east–west in this geographic area and different coastal locations are marked by different intensities (Fig. 2B). Thus, because different coastal areas have different 'magnetic signatures', animals might hypothetically use magnetic parameters to recognize a natal area (Lohmann et al., 2008a).
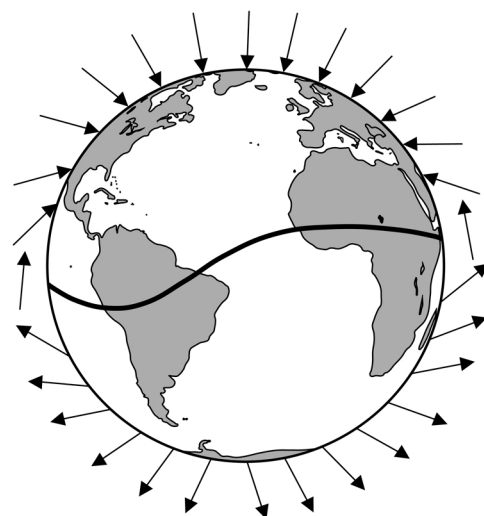

Fig. 1. Earth's magnetic field. Magnetic field lines (arrows) intersect Earth's surface, forming an inclination angle which varies with latitude. At the magnetic equator (the curving line across the planet), field lines are parallel to Earth's surface and the inclination angle is 0 deg. Field lines become progressively steeper as one moves toward the magnetic poles, where the field lines are perpendicular to Earth's surface and the inclination angle is 90 deg.
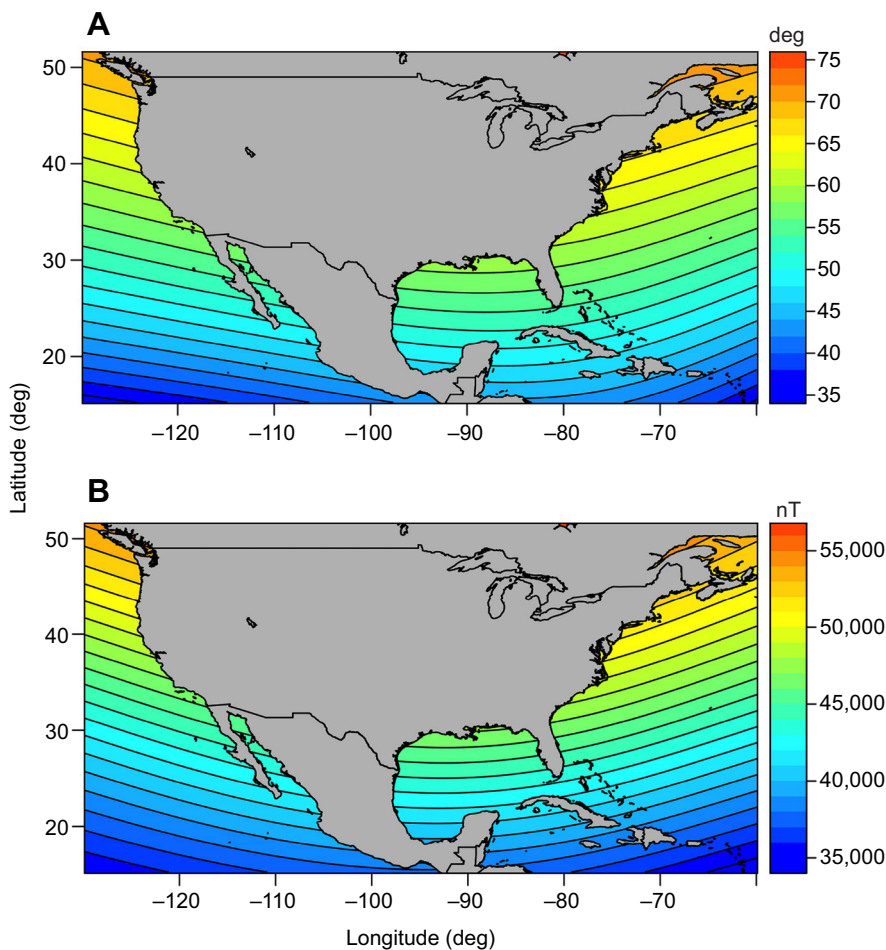
Fig. 2. Magnetic isolines along the coasts of North America. (A) Isoclinics (isolines of magnetic field inclination). Black isolines bordering each color indicate increments of 2 deg. (B) Isodynamics (isolines of total field intensity). Black isolines bordering each color indicate increments of 1000 nT. Note that each region of the west or east coast is marked by a different inclination angle and intensity. Isolines were derived from the International Geomagnetic Reference Field (IGRF) model 12 (Thébault et al., 2015) for October 2018.

There are several ways that turtles and salmon might navigate to their natal sites using magnetic information. The simplest is that, while at the natal site, the animals might imprint on a single element of the geomagnetic field (e.g. either inclination angle or intensity) at the location to which they will return. To locate the area later in life, an individual would need only to find the coastline, and then swim north or south along it to reach the target region. Alternatively, a migrant in the open ocean might seek the correct isoline and then swim along it until arriving at the coast, close to the natal area. In either case, the animal might determine whether it is north or south of the goal by assessing whether the inclination angle or intensity at a given location is greater or less than the value at the natal area. More complex possibilities also exist. For example, animals might learn both the magnetic inclination angle and intensity that exist in the home area and use the two magnetic parameters as redundant markers of the natal area or to pinpoint a location on a bi-coordinate map.

Detection of magnetic parameters for position finding

To accomplish natal homing using magnetic navigation, animals must have the ability to detect magnetic parameters that vary geographically. A lengthy series of experiments has established that hatchling loggerhead turtles can perceive both magnetic inclination angle (Lohmann and Lohmann, 1994) and magnetic field intensity (Lohmann and Lohmann, 1996b). Moreover, hatchlings exposed to magnetic fields that exist at widely separated locations along their open-sea migratory route responded by swimming in directions that would, in each case, help them advance along the migratory pathway (Lohmann et al., 2001, 2012; Fuxjager et al., 2011; Putman

et al., 2011). These results leave little doubt that turtles can distinguish among magnetic fields that exist in different geographic locations, as would be needed to identify different coastal locations on the basis of magnetic signatures.

A particularly convincing demonstration that turtles can use magnetic navigation to move toward a distant goal has come from experiments with juvenile green turtles. Turtles of this age show fidelity to coastal feeding sites and return to them after seasonal migrations or experimental displacements (Ireland, 1980; Avens et al., 2003; Avens and Lohmann, 2004). Juvenile turtles were tethered to a tracking system inside a pool of water located on land but very close to their offshore feeding area on the Atlantic coast of Florida (Lohmann et al., 2004). Turtles were then exposed to magnetic fields that exist at locations 340 km north or south of the feeding site. Individuals exposed to the northern field swam south, whereas those exposed to the southern field swam north (Fig. 3). Thus, turtles behaved as if they were trying to return home from the locations where the two fields actually exist. These findings imply that, well before the turtles mature, they have already acquired a 'magnetic map' (Lohmann et al., 2007) that can be used for navigation toward distant coastal locations.

Recent evidence suggests that salmon have sensory abilities similar to those of sea turtles. For example, juvenile Chinook salmon that had never been in the ocean responded to magnetic fields like those at the latitudinal extremes of their ocean range by orienting in directions that would, in each case, lead toward their open-sea feeding grounds (Putman et al., 2014a). To test whether the fish relied exclusively on field intensity or magnetic inclination
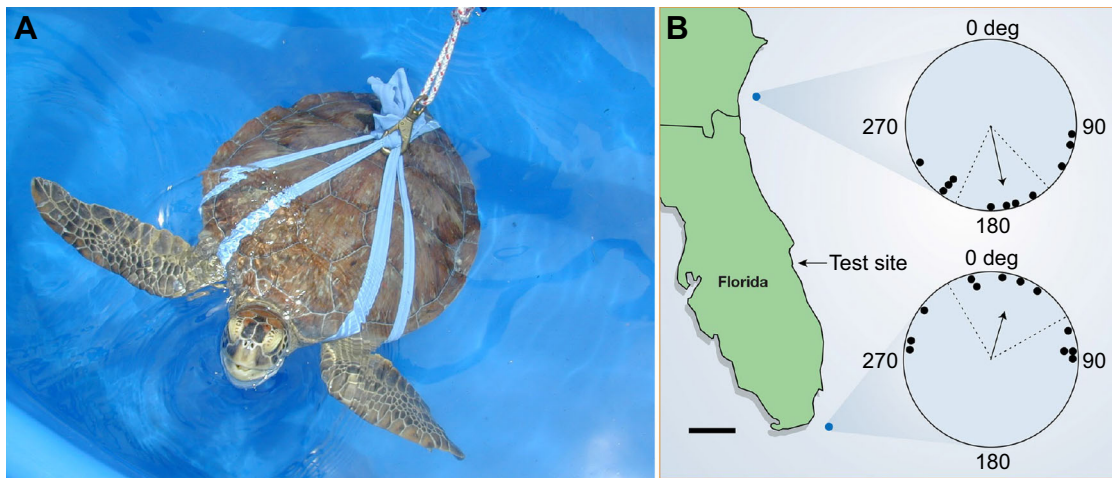
Fig. 3. Evidence for a magnetic map in green turtles. (A) A juvenile green turtle swimming in a magnetic navigation experiment. Turtles were placed into soft cloth harnesses and tethered to an electronic tracking device that monitored their orientation as they swam in a water-filled arena surrounded by a magnetic coil system (Lohmann et al., 2004). (B) Juvenile turtles were captured in feeding grounds near the test site in Florida. Each turtle was exposed to a magnetic field that exists at one of two distant locations along the coastline (represented by blue dots). Turtles exposed to the field from the northern site swam approximately southward, whereas those exposed to the field from the southern site swam approximately northward. In the orientation diagrams, each dot represents the mean angle of a single turtle. The arrow in the center of each circle represents the mean angle of the group. Dashed lines represent the 95% confidence interval for the mean angle. Figure reproduced from Lohmann et al. (2004).

angle, the intensity of the northern field was paired with the inclination of the southern field, and vice versa. If either magnetic parameter is used alone, then that parameter would be expected to dictate the response and to cause the fish in each case to perceive themselves as being north or south of the target area. Instead, fish oriented randomly in both of the two 'hybrid' fields (Putman et al., 2014a). A reasonable interpretation is that they use both inclination and intensity together to recognize the magnetic signature of an area, and that the presence of conflicting information (one parameter indicating a northern location, the other a southern location) caused confusion.

Natal homing via magnetic navigation: experiments at sea

In principle, a good way to investigate whether animals use magnetic information during natal homing is to control the magnetic fields that they encounter as they swim in the ocean toward their goal. For example, experiments could involve simulating magnetic conditions north or south of where the animals actually are, while leaving all other environmental information unchanged. Unfortunately, such an undertaking is not yet technologically feasible. A simpler approach, however, is to disrupt the magnetic field with strong magnets and determine whether changes in orientation occur when magnetic information is no longer available.

An important caveat is that disrupting the magnetic field around an animal may not have any apparent effect on the animal's migratory or homing behavior if the animal has already selected a course and has access to other sources of information that can be used to maintain a heading. For example, both sea turtles and pigeons can maintain a course using either a magnetic compass or celestial cues; impairing the ability to detect one of these simply causes the animal to use the other, without a change in orientation performance (Keeton, 1971; Avens and Lohmann, 2003; Mott and Salmon, 2011). If the animal can maintain orientation, it may even be able to reach its goal if it has access to local cues near its target.

Experiments using magnets on animals in the natural habitat have been attempted with both sea turtles and salmon. In one study (Luschi et al., 2007), nesting turtles were captured on a small island

and released approximately 100 km away with either magnets or non-magnetic brass disks on their heads. Turtles with magnets had significantly poorer homing performance than the controls. These findings are consistent with the hypothesis that turtles use magnetic information to guide movement toward a nesting beach. It is, however, impossible to infer from the results whether the effect was on the ability of turtles to: (1) hold a course using a magnetic compass; (2) navigate toward the nesting area using 'magnetic map' information; (3) recognize the nesting area on the basis of the magnetic signature; or (4) some combination of these.

Similarly, four chum salmon were tracked as they swam through the sea for several hours, during which time a small magnetic coil system attached to each fish was periodically activated (Yano et al., 1997). No obvious changes in the paths of the fish were observed when the magnetic coil system disrupted the ambient field. At the time, these results were interpreted by some as evidence that magnetic maps do not exist in salmon (e.g. Døving and Stabell, 2003), while others considered the findings to be inconclusive (e.g. Walker et al., 2003).

Natal homing to magnetic signatures: analyses of turtle nesting

Analyses of sea turtle nesting populations have provided strong circumstantial evidence that magnetic navigation plays a pivotal role in natal homing. One study exploited the fact that Earth's field is not stable, but instead changes slightly over time. This change, known as secular variation, means that magnetic isolines gradually shift position. In principle, if turtles are indeed traveling to specific magnetic signatures along the coast, then the movement of isolines might affect where turtles nest.

Along the east coast of Florida, where nearly all locations are suitable for turtle nesting, the direction and distance that an isoline moves vary among locations and years. During some years, in some locations, isolines that intersect the coastline move closer together (Fig. 4B). Under such conditions, if returning turtles seek out the magnetic signatures that mark their natal beaches, then they should nest along a shorter length of coastline, and the number of nests per
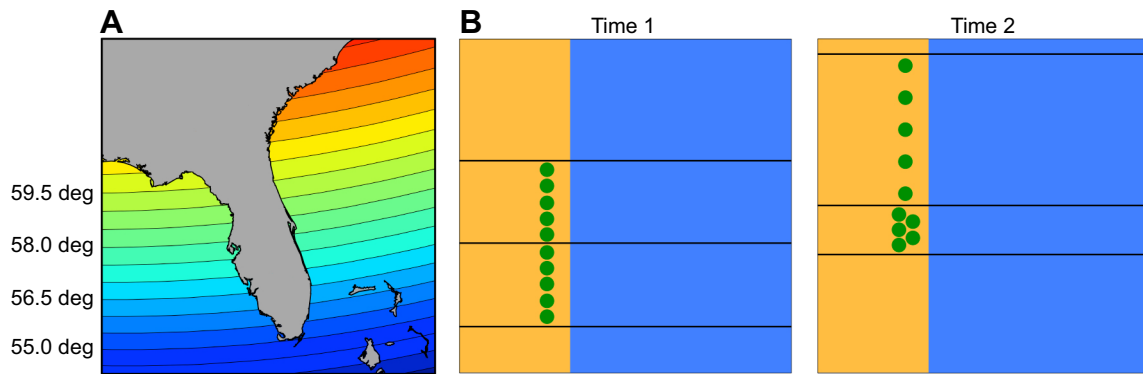
Fig. 4. Predicted effects of magnetic isoline movement on nesting density if turtles use magnetic signatures to identify natal sites. (A) Isolines of magnetic inclination along the Florida coastline. Black isolines bordering each color indicate increments of 0.5 deg and were derived from the IGRF model 11 (Finlay et al., 2010) for the year 2012. Intensity isolines are not shown but are qualitatively similar. (B) Diagrams illustrating the predicted effects of isoline movement on nesting density if geomagnetic imprinting occurs. Tan represents land; blue represents sea. Horizontal lines indicate three hypothetical isolines, and green dots represent nesting turtles, each of which has imprinted on the magnetic signature that marked her natal site as a hatchling. Over the past two decades, isolines near Florida have moved northward, but at variable rates. In some cases, isolines to the south moved less than those to the north, resulting in divergence (Time 2; upper two isolines). In these situations, the geomagnetic imprinting hypothesis predicts a decrease in nesting density, because turtles that imprinted on the fields between the isolines should return to nest over a larger area. In places where isolines converged (because those to the south moved more than those to the north), the hypothesis predicts that nesting density should increase (Time 2; lower two isolines). Modified from Brothers and Lohmann (2015).

unit distance should increase (Fig. 4B). By contrast, isolines along the coast can also move apart. Under these conditions, returning turtles would be expected to nest over a slightly greater length of coastline, and nesting density would be expected to decrease (Fig. 4B). An analysis of a 19-year database of loggerhead turtle nesting along the east coast of Florida (Brothers and Lohmann, 2015) confirmed these predictions (Fig. 5), thus providing indirect evidence that adult turtles locate their natal beaches by seeking out specific magnetic signatures.

Additional evidence that nesting female turtles seek out magnetic signatures has emerged from studies of population genetics (Shamblin et al., 2011; Lohmann et al., 2013; Brothers and Lohmann, 2018). Analyses have revealed that loggerhead turtles that nest at similar latitudes but on opposite sides of the Florida peninsula are often genetically similar despite their geographic distance from each other (Shamblin et al., 2011). Given that the magnetic fields at latitudinally similar locations on opposite sides of
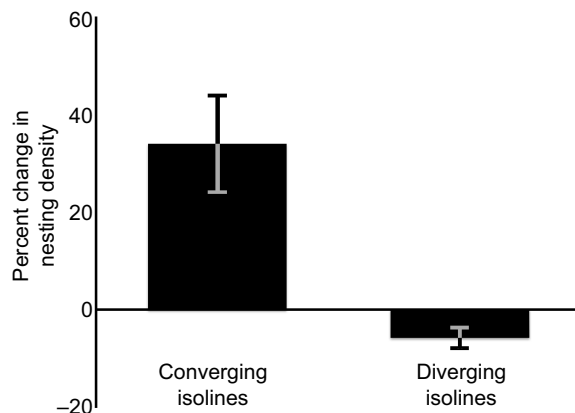

Fig. 5. Changes in nesting density for coastal areas with converging and diverging inclination isolines. At times and places in which isolines of inclination converged, nesting density increased by an average of 35%. At times and places in which isolines diverged, nesting density decreased by an average of 6%. The mean changes of the two groups were significantly different. Error bars represent s.e.m. Figure reproduced from Brothers and Lohmann (2015).

Florida are similar, an interesting possibility is that this population structure has arisen as a consequence of errors in magnetic navigation during natal homing (Shamblin et al., 2011; Lohmann et al., 2013). In other words, if turtles seek out the magnetic signature of their natal beach, but sometimes mistakenly nest on a different beach with a similar magnetic signature, then the genetic pattern can be readily explained. Consistent with this possibility, some loggerhead turtles nest in widely separated locations during their lifetimes, including sites on both the east and west coasts of Florida (Bjorndal et al., 1983).

In a recent study (Brothers and Lohmann, 2018), the population structure of loggerhead turtles at nesting beaches throughout the southeastern US was analyzed in the context of the magnetic signatures that exist at each beach. Specifically, F_{ST} values were obtained from pairwise comparisons between each possible combination of nesting beaches. F_{ST} is a widely used metric that ranges from zero to one, with low values indicating genetic similarity and high values indicating genetic differentiation. For each combination of nesting beaches, the difference between the magnetic fields at the two locations was also calculated, as were metrics of environmental similarity and geographic distance.

Analyses revealed a striking relationship between genetic differentiation, as estimated by F_{ST}, and spatial variation in Earth's magnetic field (Fig. 6). Populations of turtles nesting at beaches with similar magnetic fields tended to be genetically similar, whereas nesting populations at beaches marked by larger differences in magnetic fields had greater genetic differences. This relationship held even when environmental similarities and geographic distance were taken into account. These results provide strong evidence that spatial variation in Earth's magnetic field influences spatial genetic variation in loggerhead turtles, through a process most likely mediated by magnetic navigation and geomagnetic imprinting.

Natal homing to magnetic signatures: studies of salmon homing

In a modeling study, Bracis and Anderson (2012) investigated whether simple magnetic navigational strategies, combined with geomagnetic imprinting, might be sufficient to guide spring Chinook salmon from the open Pacific back to the Columbia
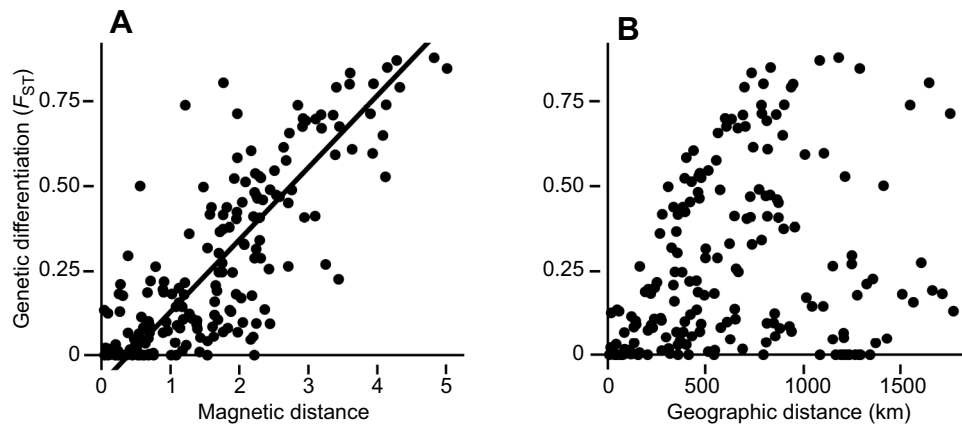
Fig. 6. Effects of magnetic distance and geographic distance on population structure of loggerhead turtles in Florida. (A) Regression analysis showing the relationship between F_{ST} and magnetic distance. Magnetic distance is a metric that reflects the difference in magnetic fields between two nesting locations; a low magnetic distance implies that the magnetic fields at the two beaches are very similar, while a high magnetic distance implies a large difference in magnetic fields. A single metric for magnetic distance was used because inclination and intensity co-vary over the study area. Each data point represents a pairwise comparison between two nesting beaches, with the genetic differentiation between nesting beaches on the y-axis and the magnetic distance on the x-axis. A strong positive relationship exists between magnetic distance and genetic differentiation (P=0.001). Nesting beaches with similar magnetic fields harbor populations of turtles that are genetically similar, whereas nesting beaches with different magnetic fields are home to populations of turtles that are genetically distinct. (B) Regression analysis showing the relationship between F_{ST} and geographic distance. No significant relationship was found between F_{ST} and geographic distance (the distance a turtle would need to swim to go from one of the two nesting beaches to the other). Modified from Brothers and Lohmann (2018).

River during their spawning migration. The results demonstrated that approaching a specific magnetic isoline and then swimming along it could successfully return most fish to the appropriate coastal area. Although inclination angle appeared to be a more robust cue than intensity, either could hypothetically be used.

A subsequent study investigated paths of migrating salmon in the Bering Sea (Azumaya et al., 2016). Archival tags that recorded the ambient magnetic field were attached to several chum salmon captured early in the spawning migration. The fish were released near the site of capture; two were later recaptured near the coast of Hokkaido, Japan, after migrations that exceeded 2000 km. The reconstructed homing routes were consistent with a strategy of following magnetic isolines rather than a great circle route (which would have yielded the shortest path). Moreover, the path of one of the fish was approximately along the intensity isoline that existed at the coastal recapture site. The authors suggested a possible role of magnetic intensity in guiding the homing migration of chum salmon in the open sea.

Additional evidence consistent with the geomagnetic imprinting hypothesis has come from analyses of fisheries data involving sockeye salmon (Putman et al., 2014a,b). This species homes to its natal river system (Quinn, 2005) and is known to have a magnetic compass sense (Quinn, 1980; Quinn and Brannon, 1982). Sockeye salmon from the Fraser River of British Columbia, Canada, typically spend 2 years at sea dispersed throughout the Gulf of Alaska before the onset of their homeward migration (Burgner, 1991; Groot and Quinn, 1987). Their return to the Fraser River requires a detour around Vancouver Island, via either a southern route through the Strait of Juan de Fuca or a northern route through Queen Charlotte Strait (Fig. 7A).

The geographical constraint imposed by Vancouver Island, combined with the existence of five decades of fisheries data on the proportion of sockeye that used each route each year, provided a unique opportunity to test the geomagnetic imprinting hypothesis (Putman et al., 2013). If salmon imprint on the magnetic field at the river mouth where they begin their oceanic phase (Lohmann et al., 2008a), then whether fish return by the northern or southern route

might be influenced by subtle changes in Earth's field near Vancouver Island. Specifically, the route each year might reflect how closely the field at each entryway, at the time of return, resembles the magnetic signature that fish are seeking – that is, the field the fish experienced when leaving the Fraser River 2 years previously. If geomagnetic imprinting occurs, then a greater proportion of fish would be expected to use the northern route when the magnetic field at the northern entryway closely resembles the original Fraser River signature. By contrast, when the magnetic field at the southern entryway closely matches the original Fraser River signature, a greater proportion of fish would be expected to take the southern route.

The analysis revealed that, when the magnetic intensity at the Fraser River and northern entry were similar, a higher proportion of sockeye salmon did indeed migrate through the northern route (Putman et al., 2013; see Fig. 7B). Likewise, when the magnetic intensity at the Fraser River and the southern entryway became similar, a higher proportion of salmon migrated through the southern route (Fig. 7C). The difference in magnetic inclination angle between the northern entryway and the Fraser River also correlated with use of that entryway, though the same relationship was not observed at the southern entryway. Other environmental factors were also correlated with the return route of the salmon. For example, in years with higher sea surface temperature, a higher proportion of salmon migrated through the northern route, possibly because the salmon spent more time in northern waters when temperatures to the south were warmer. Regardless, this study and additional analyses of sockeye and pink salmon (*Onchorhynchus gorbuscha*) (Putman et al., 2013, 2014b) indicate that subtle changes in the local magnetic field affect natal homing.

Natal homing to magnetic signatures: effects of secular variation

In principle, secular variation might complicate the strategy of using magnetic signatures to locate natal areas, because field changes that occur at the natal site during an animal's absence might cause navigational errors during return migrations. On the Atlantic coast
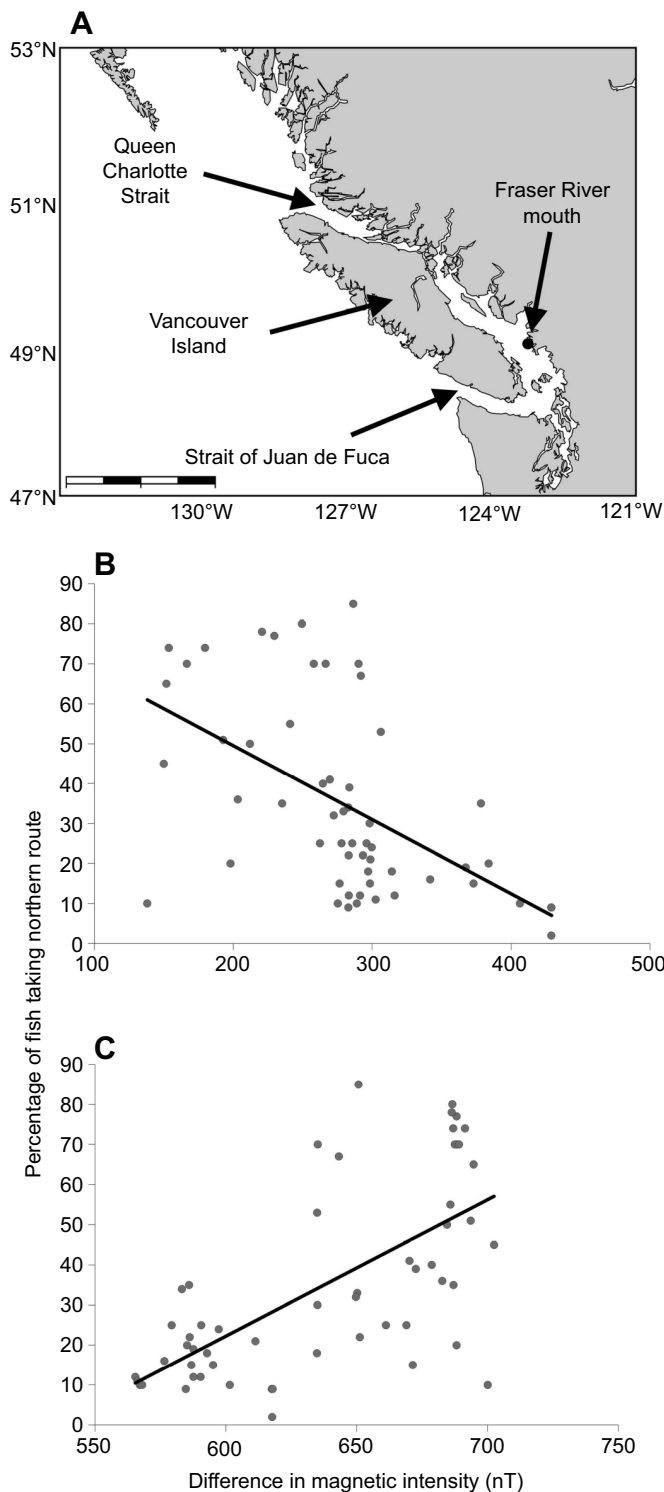
Fig. 7. Evidence that salmon navigate to the vicinity of their natal rivers using magnetic signatures. (A) Map of Vancouver Island showing possible routes that salmon can follow to reach the Fraser River during their spawning migrations. Fish attempting to return to the Fraser River must travel around Vancouver Island via either a northern route through Queen Charlotte Strait or via a southern route through the Strait of Juan de Fuca. Scale bar represents 225 km. (B) Relationship between the percentage of fish using the northern migratory route and the difference in magnetic intensity between the mouth of the Fraser River at the time when the fish departed the river and the magnetic intensity of the northern passage at the time when the fish returned. Each data point represents a different year. In years when the difference between the two was low, the percentage of fish that took the northern route tended to be high; when the difference was high, the percentage of fish that took the northern route tended to be low. (C) Relationship between the percentage of salmon taking the northern route and the difference in magnetic intensity between the mouth of the Fraser River and the southern passage. In years when the difference in magnetic intensity between the two locations was low, the percentage of fish taking the northern route tended to be low, but when the difference was high, the percentage of fish taking the northern route tended to be high. Modified from Putman et al. (2013).

Quantifying the effect of secular variation on navigation is challenging, in part because the rate of field change varies among different geographic regions and at different points in time. Several simple modeling exercises, however, imply that geomagnetic imprinting is compatible with current and recent rates of field change. For example, salmon that reproduce in the Columbia River typically return to the river after about 3 years at sea (Dittman and Quinn, 1996; Bigler et al., 1996). Analyses indicate that navigational errors of returning salmon would have averaged about 6 km over the past century if the fish imprinted on the inclination angle at the river mouth, and about 31 km if they imprinted on total intensity (Lohmann et al., 2008b). Thus, a strategy of imprinting on the magnetic field near the river mouth can hypothetically enable salmon to return to the vicinity of the Columbia River, close enough for the fish to find the river mouth using olfactory or other cues.

Among sea turtles, different populations and species reach maturity at very different ages. For example, Kemp's ridley turtles are thought to mature in as little as a decade (Plotkin, 2007), whereas loggerhead and green turtles in some areas can require approximately 30 years (Avens and Snover, 2013). Nevertheless, an analysis of navigational errors that might occur at three major, widely separated continental nesting beaches suggests that simple strategies of geomagnetic imprinting can return turtles to an appropriate geographic region, even after an absence of a decade or more (Lohmann et al., 2008a).

The 30 km nesting area of the Kemp's ridley turtle has been studied particularly thoroughly in this regard (Putman and Lohmann, 2008). Analyses indicate that if a Kemp's ridley turtle were to imprint on magnetic inclination angle as a hatchling and return after a decade to the coastal location with the same angle, then the turtle would, on average, arrive approximately 23 km from its precise natal site (Putman and Lohmann, 2008). This would typically bring the turtle to a location within the area of beach used for nesting, or at least close enough to locate the area using additional, local cues. Moreover, if turtles update their knowledge of the magnetic field at the nesting beach each time they visit, then secular variation might have a smaller effect on subsequent return trips, given that female turtles typically nest every 2–4 years once they reach maturity (Lohmann et al., 1999).

In addition, some turtles are not absent from the natal beach region for the entire maturation period. For example, juvenile loggerhead turtles show natal homing on a regional scale well before

of Florida, such errors might have little consequence for sea turtles because nearly all beaches are suitable for nesting. For species and populations where the target is more restricted, however, the potential for negative consequences is greater. Nonetheless, analyses suggest that navigational errors attributable to secular variation will not typically prevent animals from returning to the general area of their natal sites, close enough for local cues to guide migrants to their final destinations (Lohmann et al., 1999, 2008a; Putman and Lohmann, 2008).

their first reproductive migration (Bowen et al., 2004). When these turtles leave the open ocean to establish coastal feeding sites, they choose foraging grounds within their general natal region more often than would be expected by chance (Bowen et al., 2004; Bowen and Karl, 2007). This regional homing raises the possibility that loggerhead turtles diminish effects of secular variation on natal homing accuracy by updating their knowledge of the field in their natal region long before their first reproductive migration (Putman and Lohmann, 2008; Lohmann et al., 2008a).

Island-nesting turtles and geomagnetic imprinting

Although most beaches with large numbers of nesting sea turtles are located along continental coastlines, some turtle populations nest on islands. From an evolutionary perspective, island-nesting populations are thought to be derived from turtles that originally nested on continents (Bowen and Karl, 2007). Whether turtles in the two groups use the same mechanisms to locate their natal areas is not known. Alternative strategies of navigation and imprinting might have evolved to facilitate island nesting; indeed, the mechanisms used by any population to return to a natal area might depend in part on what is effective in a particular geographic setting (Lohmann et al., 2007, 2008a).

In principle, finding an island using a single magnetic element such as inclination or intensity is possible, inasmuch as a turtle might follow an isoline that intersects the island or passes nearby (Lohmann et al., 2007). Thus, a combination of geomagnetic imprinting and magnetic navigation similar to that outlined previously for continental nesting sites might suffice in some cases. Alternatively or additionally, a more complex strategy, such as imprinting on two elements of the field and using some form of bi-coordinate magnetic navigation, might also be feasible in some situations (Lohmann et al., 1999, 2007, 2008a). Simulations have indicated that a strategy of using magnetic navigation to arrive in the vicinity of an island, and then using chemical cues to pinpoint it, is plausible even for very small, remote islands, and even when significant secular variation occurs (Endres et al., 2016). Additional environmental cues such as the sound of waves breaking or the pattern of waves refracting around an island might also help turtles locate islands once they have drawn near (Lohmann et al., 1999, 2008c).

Natal homing without geomagnetic imprinting?

Although the totality of evidence strongly implies that salmon and sea turtles use magnetic navigation to home to a specific magnetic signature, an interesting question is whether the process of imprinting must be invoked (Lohmann et al., 2013). At least two alternatives to geomagnetic imprinting hypothetically exist: (1) the animals might use inherited rather than learned magnetic information to find the natal area; and (2) animals might learn the magnetic signature of the natal area, but through a process that does not meet the strict ethological definition of imprinting.

Several factors suggest that salmon and turtles probably do not inherit knowledge of the magnetic signature at the natal location. One consideration is that, if animals were genetically programmed to return to the magnetic signature of an ancestral reproductive area, then navigational errors resulting from secular variation would presumably increase in magnitude with each generation. Moreover, offspring would have no way to adjust rapidly to changed circumstances; for example, if an ancestral nesting beach is destroyed by a hurricane so that returning turtles are forced to nest in a new location, their offspring would nevertheless still be programmed to return to the ancestral site. For these reasons, a flexible system based on imprinting may confer significant

advantages, one of which is the ability to colonize new areas rapidly when necessary (Lohmann et al., 2013).

Perhaps the most compelling evidence that imprinting plays a role in natal homing is that it has proven possible to establish populations of salmon and sea turtles in new geographic areas (Harache, 1992; Shaver and Wibbels, 2007; Crawford and Muir, 2008; Shaver and Caillouet, 2015). In these instances, young animals were raised and/ or released in the new locations, and many subsequently returned to reproduce there as adults, rather than migrating to the areas from which their parents originated. Such an outcome would presumably not have occurred if the animals were hardwired to return to a particular magnetic signature.

If salmon and turtles do indeed learn magnetic signatures, the process of learning might or might not fully meet the definition of imprinting. The hallmarks of imprinting are that the learning occurs during a specific, critical period, the effects are long lasting, and the learning cannot be easily modified (e.g. Hasler and Scholz, 1983; Alcock, 2009; Zupanc, 2010; Goodenough et al., 2010). Although experiments are lacking, circumstances suggest that salmon might plausibly meet all three criteria. Most salmon leave the natal river or stream and enter the sea only once before returning a single time to spawn and die. Thus, the initial entry to the sea represents the only opportunity to learn the magnetic signature of the river mouth, and the natal homing behavior is consistent with a long-lasting, seemingly permanent learning event that occurs at a critical point in the animal's life.

In contrast to salmon, female sea turtles nest repeatedly over a period of years. Thus, they return to their natal area multiple times and have additional opportunities for learning that salmon lack. In principle, instead of imprinting on the magnetic signature of the beach as hatchlings, turtles might instead learn it when they return for the first time as adults, provided that they can somehow reach the natal beach the first time without relying on magnetic information – for example, by following experienced nesters to the nesting area. Although no evidence for such 'socially facilitated' migration presently exists (Meylan et al., 1990; Plotkin et al., 1995), this and other alternatives to imprinting warrant further study.

Summary and future directions

Natal homing is a central element of the life history of numerous long-distance migrants. It presumably functions to return animals to habitats that possess environmental factors necessary for successful reproduction (Lohmann et al., 2008a, 2013). Despite the prevalence of natal homing, the mechanisms underlying it have received little attention, with the single notable exception of olfactory imprinting in salmon.

During the past decade, new approaches have provided the first glimpse into the mechanistic underpinnings of long-distance natal homing in two phylogenetically different groups of marine migrants. Sea turtles are secondarily marine, having descended from terrestrial reptiles, while salmon, being fish, lack terrestrial ancestors. It is striking to note that, despite their disparate evolutionary histories, sea turtles and salmon appear to accomplish natal homing in a similar way. A variety of experimental results, population analyses and theoretical considerations are consistent with the view that both groups rely primarily on geomagnetic imprinting and magnetic navigation to reach the vicinity of a natal area, and then rely on local cues (chemical or otherwise) to reach their target. It thus appears plausible that these same mechanisms underlie natal homing in diverse marine migrants such as tuna, sharks, elephant seals and whales, and perhaps also exist in some terrestrial migrants such as birds.

References

Alcock, J. (2009). *Animal Behavior: an Evolutionary Approach*, 9th edn. Sunderland: Sinauer Associates.

Avens, L. and Lohmann, K. J. (2003). Use of multiple orientation cues by juvenile loggerhead sea turtles *Caretta caretta*. *J. Exp. Biol.* **206**, 4317-4325.

Avens, L. and Lohmann, K. J. (2004). Navigation and seasonal migratory orientation in juvenile sea turtles. *J. Exp. Biol.* **207**, 1771-1778.

Avens, L. and Snover, M. (2013). Age and age estimation in sea turtles. In *The Biology of Sea Turtles Volume III* (ed. J. Wyneken, K. J. Lohmann and J. A. Musick), pp. 97-134. Boca Raton: CRC Press.

Avens, L., Braun-McNeill, J., Epperly, S. and Lohmann, K. J. (2003). Site fidelity and homing behavior in juvenile loggerhead sea turtles (*Caretta caretta*). *Mar. Biol.* **143**, 211-220.

Azumaya, T., Sato, S., Urawa, S. and Nagasawa, T. (2016). Potential role of the magnetic field on homing in chum salmon (*Oncorhynchus keta*) tracked from the open sea to coastal Japan. *North Pacific Anadromous Fish Comm. Bull.* **6**, 235-241.

Baker, C. S., Steel, D., Calambokidis, J., Falcone, E., González-Peral, U., Barlow, J., Burdin, A. M., Clapham, P. J., Ford, J. K. B., Gabriele, C. M. et al. (2013). Strong maternal fidelity and natal philopatry shape genetic structure in North Pacific humpback whales. *Mar. Ecol. Prog. Ser.* **494**, 291-306.

Bigler, B. S., Welch, D. W. and Helle, J. H. (1996). A review of size trends among North Pacific salmon (*Oncorhynchus* spp.). *Can. J. Fish. Aquat. Sci.* **53**, 455-465.

Bjorndal, K. A., Meylan, A. B. and Turner, B. J. (1983). Sea turtles nesting at Melbourne Beach, Florida, I. Size, growth and reproductive biology. *Biol. Conserv.* **26**, 65-77.

Bjorndal, K. A., Bolten, A. B. and Martins, H. R. (2000). Somatic growth model of juvenile loggerhead sea turtles *Caretta caretta*: duration of pelagic stage. *Mar. Ecol. Prog. Ser.* **202**, 265-272.

Bowen, B. W. and Avise, J. C. (1995). Conservation genetics of marine turtles. In *Conservation Genetics: Case Histories from Nature* (ed. J. C. Avise and J. L. Hamrick), pp. 190-237. New York: Chapman and Hall.

Bowen, B. W. and Karl, S. A. (2007). Population genetics and phylogeography of sea turtles. *Mol. Ecol.* **16**, 4886-4907.

Bowen, B. W., Bass, A. L., Chow, S.-M., Bostrom, M., Bjorndal, K. A., Bolten, A. B., Okuyama, T., Bolker, B. M., Epperly, S., Lacasella, E. et al. (2004). Natal homing in juvenile loggerhead turtles (*Caretta caretta*). *Mol. Ecol.* **13**, 3797-3808.

Bracis, C. and Anderson, J. J. (2012). An investigation of the geomagnetic imprinting hypothesis for salmon. *Fish. Oceanogr.* **21**, 170-181.

Brothers, J. R. and Lohmann, K. J. (2015). Evidence for geomagnetic imprinting and magnetic navigation in the natal homing of sea turtles. *Curr. Biol.* **25**, 392-396.

Brothers, J. R. and Lohmann, K. J. (2018). Evidence that magnetic navigation and geomagnetic imprinting shape spatial genetic variation in sea turtles. *Curr. Biol.* **28**, 1325-1329.

Burgner, R. L. (1991). Life history of sockeye salmon, *Oncorhynchus nerka*. In *Pacific Salmon Life Histories* (ed. C. Groot and L. Margolis), pp. 1-118. Vancouver, BC: UBC Press.

Crawford, S. S. and Muir, A. M. (2008). Global introductions of salmon and trout in the genus *Oncorhynchus*: 1870–2007. *Rev. Fish Biol. Fish.* **18**, 313-344.

Dittman, A. and Quinn, T. (1996). Homing in Pacific salmon: mechanisms and ecological basis. *J. Exp. Biol.* **199**, 83-91.

Dittman, A. H., Quinn, T. P. and Nevitt, G. A. (1996). Timing of imprinting to natural and artificial odors by coho salmon (*Oncorhynchus kisutch*). *Can. J. Fish. Aquat. Sci.* **53**, 434-442.

Døving, K. B. and Stabell, O. B. (2003). Trails in open waters: sensory cues in salmon migration. In *Sensory Processing in Aquatic Environments* (ed. S. P. Collin and N. J. Marshall), pp. 39-52. New York, NY: Springer New York.

Endres, C. S. and Lohmann, K. J. (2012). Perception of dimethyl sulfide (DMS) by loggerhead sea turtles: a possible mechanism for locating high-productivity oceanic regions for foraging. *J. Exp. Biol.* **215**, 3535-3538.

Endres, C. S. and Lohmann, K. J. (2013). Detection of coastal mud odors by loggerhead sea turtles: a possible mechanism for sensing nearby land. *Mar. Biol.* **160**, 2951-2956.

Endres, C. S., Putman, N. F., Ernst, D. A., Kurth, J. A., Lohmann, C. M. F. and Lohmann, K. J. (2016). Multi-modal homing in sea turtles: modeling dual use of geomagnetic and chemical cues in island-finding. *Front. Behav. Neurosci.* **10**, 19.

Feldheim, K. A., Gruber, S. H., DiBattista, J. D., Babcock, E. A., Kessel, S. T., Hendry, A. P., Pikitch, E. K., Ashley, M. V. and Chapman, D. D. (2014). Two decades of genetic profiling yields first evidence of natal philopatry and long-term fidelity to parturition sites in sharks. *Mol. Ecol.* **23**, 110-117.

Finlay, C. C., Maus, S., Beggan, C. D., Bondar, T. N., Chambodut, A., Chernova, T. A., Chulliat, A., Golovkov, V. P., Hamilton, B., Hamoudi, M. et al. (2010). International geomagnetic reference field: the eleventh generation. *Geophys. J. Int.* **183**, 1216-1230.

Fuxjager, M. J., Eastwood, B. S. and Lohmann, K. J. (2011). Orientation of hatchling loggerhead sea turtles to regional magnetic fields along a transoceanic migratory pathway. *J. Exp. Biol.* **214**, 2504-2508.

Goodenough, J., McGuire, B. and Jakob, E. M. (2010). *Perspectives on Animal Behavior*, 3rd edn. Hoboken: J. Wiley and Sons.

Grassman, M. A., Owens, D. W., McVey, J. P. and Marquez, R. (1984). Olfactory-based orientation in artificially imprinted sea turtles. *Science* **224**, 83-84.

Groot, C. and Margolis, L. (ed.) (1991). *Pacific Salmon Life Histories*. Vancouver: UBC Press.

Groot, C. and Quinn, T. P. (1987). Homing migration of sockeye salmon, *Oncorhynchus nerka*, to the Fraser River. *Fish. Bull.* **85**, 455-469.

Groot, C., Quinn, T. P. and Hara, T. J. (1986). Responses of migrating adult sockeye salmon (*Oncorhynchus nerka*) to population-specific odours. *Can. J. Zool.* **64**, 926-932.

Harache, Y. (1992). Pacific salmon in Atlantic waters. *ICES Mar. Sci. Symp.* **194**, 1955-1977.

Hasler, A. D. (1971). Orientation and fish migration. In *Fish Physiology*, Vol. 6 (ed. W. S. Hoar and D. J. Randall), pp. 429-510. New York: Academic Press.

Hasler, A. D. and Scholz, A. T. (1983). *Olfactory Imprinting and Homing in Salmon*. Berlin: Springer-Verlag.

Ireland, L. C. (1980). Homing behavior of juvenile green turtles, *Chelonia mydas*. In *A Handbook on Biotelemetry and Radio Tracking* (ed. C. J. Amlaner, Jr and D. W. MacDonald), pp. 761-764. Oxford, UK: Pergamon Press.

Keeton, W. T. (1971). Magnets interfere with pigeon homing. *Proc. Natl. Acad. Sci. USA* **68**, 102-106.

Lohmann, K. J. (1991). Magnetic orientation by hatchling loggerhead sea turtles (*Caretta caretta*). *J. Exp. Biol.* **155**, 37-49.

Lohmann, K. J. and Lohmann, C. M. F. (1993). A light-independent magnetic compass in the leatherback sea turtle. *Biol. Bull.* **185**, 149-151.

Lohmann, K. J. and Lohmann, C. M. F. (1994). Detection of magnetic inclination angle by sea turtles: a possible mechanism for determining latitude. *J. Exp. Biol.* **194**, 23-32.

Lohmann, K. J. and Lohmann, C. M. F. (1996a). Orientation and open-sea navigation of sea turtles. *J. Exp. Biol.* **199**, 73-81.

Lohmann, K. J. and Lohmann, C. M. F. (1996b). Detection of magnetic field intensity by sea turtles. *Nature* **380**, 59-61.

Lohmann, K. J. and Lohmann, C. M. F. (2003). Orientation mechanisms of hatchling loggerheads. In *Loggerhead Sea Turtles* (ed. A. Bolten and B. Witherington), pp. 44-62. Washington, DC: Smithsonian Institution Press.

Lohmann, K. J., Hester, J. T. and Lohmann, C. M. F. (1999). Long-distance navigation in sea turtles. *Ethol. Ecol. Evol.* **11**, 1-23.

Lohmann, K. J., Cain, S. D., Dodge, S. A. and Lohmann, C. M. F. (2001). Regional magnetic fields as navigational markers for sea turtles. *Science* **294**, 364-366.

Lohmann, K. J., Lohmann, C. M. F., Ehrhart, L. M., Bagley, D. A. and Swing, T. (2004). Geomagnetic map used in sea-turtle navigation. *Nature* **428**, 909-910.

Lohmann, K. J., Lohmann, C. M. F. and Putman, N. F. (2007). Magnetic maps in animals: nature's GPS. *J. Exp. Biol.* **210**, 3697-3705.

Lohmann, K. J., Putman, N. F. and 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**, 19096-19101.

Lohmann, K. J., Lohmann, C. M. F. and Endres, C. S. (2008b). The sensory ecology of ocean navigation. *J. Exp. Biol.* **211**, 1719-1728.

Lohmann, K. J., Luschi, P. and Hays, G. C. (2008c). Goal navigation and island-finding in sea turtles. *J. Exp. Mar. Biol. Ecol.* **356**, 83-95.

Lohmann, K. J., Putman, N. F. and Lohmann, C. M. F. (2012). The magnetic map of hatchling loggerhead sea turtles. *Curr. Opin. Neurobiol.* **22**, 336-342.

Lohmann, K. J., Lohmann, C. M. F., Brothers, J. R. and Putman, N. F. (2013). Natal homing and imprinting in sea turtles. In *The Biology of Sea Turtles*, Vol. III (ed. J. Wyneken, K. J. Lohmann and J. A. Musick), pp. 59-77. Boca Raton: CRC Press.

Luschi, P., Benhamou, S., Girard, C., Ciccione, S., Roos, D., Sudre, J. and Benvenuti, S. (2007). Marine turtles use geomagnetic cues during open-sea homing. *Curr. Biol.* **17**, 126-133.

Lutz, P. L. and Musick, J. A. (ed.) (1997). *The Biology of Sea Turtles*. Boca Raton: CRC Press.

Mansfield, K. L. and Putman, N. F. (2013). Oceanic habits and habitats - *Caretta caretta*. In *The Biology of Sea Turtles*, Vol. III (ed. J. Wyneken, K. J. Lohmann and J. A. Musick), pp. 163-188. Boca Raton: CRC Press.

Manton, M. L., Karr, A. and Ehrenfeld, D. W. (1972a). An operant method for the study of chemoreception in the green turtle, *Chelonia mydas*. *Brain. Behav. Evol.* **5**, 188-201.

Manton, M. L., Karr, A. and Ehrenfeld, D. W. (1972b). Chemoreception in the migratory sea turtle *Chelonia mydas*. *Biol. Bull.* **143**, 184-195.

Meylan, A., Bowen, B. and Avise, J. (1990). A genetic test of the natal homing versus social facilitation models for green turtle migration. *Science* **248**, 724-727.

Mott, C. R. and Salmon, M. (2011). Sun compass orientation by juvenile green sea turtles (*Chelonia mydas*). *Chelonian Conserv. Biol.* **10**, 73-81.

Mouritsen, H. (2018). Long-distance navigation and magnetoreception in migratory animals. *Nature* **558**, 50-59.

Nevitt, G. and Dittman, A. (1998). A new model for olfactory imprinting in salmon. *Integr. Biol. Issues News Rev.* **1**, 215-223.

Nordeng, H. (1971). Is the local orientation of anadromous fishes determined by pheromones? *Nature* **233**, 411-413.

Plotkin, P. (ed.) (2007). *Biology and Conservation of Ridley Sea Turtles*. Baltimore: The Johns Hopkins University Press.

Plotkin, P. T., Byles, R. A., Rostal, D. C. and Owens, D. W. (1995). Independent versus socially facilitated oceanic migrations of the olive ridley, *Lepidochelys olivacea*. *Mar. Biol.* **122**, 137-143.

Putman, N. F. and Lohmann, K. J. (2008). Compatibility of magnetic imprinting and secular variation. *Curr. Biol.* **18**, R596-R597.

Putman, N. F., Endres, C. S., Lohmann, C. M. F. and Lohmann, K. J. (2011). Longitude perception and bicoordinate magnetic maps in sea turtles. *Curr. Biol.* **21**, 463-466.

Putman, N. F., Lohmann, K. J., Putman, E. M., Quinn, T. P., Klimley, A. P. and Noakes, D. L. G. (2013). Evidence for geomagnetic imprinting as a homing mechanism in Pacific salmon. *Curr. Biol.* **23**, 312-316.

Putman, N. F., Scanlan, M. M., Billman, E. J., O'Neil, J. P., Couture, R. B., Quinn, T. P., Lohmann, K. J. and Noakes, D. L. G. (2014a). An inherited magnetic map guides ocean navigation in juvenile Pacific salmon. *Curr. Biol.* **24**, 446-450.

Putman, N. F., Jenkins, E. S., Michielsens, C. G. J. and Noakes, D. L. G. (2014b). Geomagnetic imprinting predicts spatio-temporal variation in homing migration of pink and sockeye salmon. *J. R. Soc. Interface* **11**, 20140542.

Quinn, T. P. (1980). Evidence for celestial and magnetic compass orientation in lake migrating sockeye salmon fry. *J. Comp. Physiol.* **137**, 243-248.

Quinn, T. P. (2005). *The Behavior and Ecology of Pacific Salmon and Trout*. University of Washington Press.

Quinn, T. P. and Brannon, E. L. (1982). The use of celestial and magnetic cues by orienting sockeye salmon smolts. *J. Comp. Physiol.* **147**, 547-552.

Quinn, T. P., Volk, E. C. and Hendry, A. P. (1999). Natural otolith microstructure patterns reveal precise homing to natal incubation sites by sockeye salmon (*Oncorhynchus nerka*). *Can. J. Zool.* **77**, 766-775.

Rooker, J. R., Secor, D. H., De Metrio, G., Schloesser, R., Block, B. A. and Neilson, J. D. (2008). Natal homing and connectivity in Atlantic bluefin tuna populations. *Science* **322**, 742-744.

Shamblin, B. M., Dodd, M. G., Bagley, D. A., Ehrhart, L. M., Tucker, A. D., Johnson, C., Carthy, R. R., Scarpino, R. A., McMichael, E., Addison, D. S. et al. (2011). Genetic structure of the southeastern United States loggerhead turtle nesting aggregation: evidence of additional structure within the peninsular Florida recovery unit. *Mar. Biol.* **158**, 571-587.

Shaver, D. J. and Caillouet, C. W. (2015). Reintroduction of Kemp's ridley (*Lepidochelys kempii*) sea turtle to Padre Island National Seashore, Texas and its connection to head-starting. *Herpetol. Conserv. Biol.* **10**, 378-435.

Shaver, D. J. and Wibbels, T. (2007). Head-starting the Kemp's ridley sea turtle. In *Biology and Conservation of Ridley Sea Turtles* (ed. P. Plotkin), pp. 297-323. Baltimore: The Johns Hopkins University Press.

Thébault, E., Finlay, C. C., Beggan, C. D., Alken, P., Aubert, J., Barrois, O., Bertrand, F., Bondar, T., Boness, A., Brocco, L. et al. (2015). International geomagnetic reference field: the 12th generation. *Earth Planets Space* **67**, 79.

van Buskirk, J. and Crowder, L. B. (1994). Life-history variation in marine turtles. *Copeia* **1994**, 66-81.

Walker, M. M., Diebel, C. E. and Kirschvink, J. L. (2003). Detection and use of the earth's magnetic field by aquatic vertebrates. In *Sensory Processing in Aquatic Environments* (ed. S. P. Collin and N. J. Marshall), pp. 53-74. New York, NY: Springer New York.

Welch, A. J., Fleischer, R. C., James, H. F., Wiley, A. E., Ostrom, P. H., Adams, J., Duvall, F., Holmes, N., Hu, D., Penniman, J. et al. (2012). Population divergence and gene flow in an endangered and highly mobile seabird. *Heredity* **109**, 19-28.

Wheelwright, N. T. and Mauck, R. A. (1998). Philopatry, natal dispersal, and inbreeding avoidance in an island population of savannah sparrows. *Ecology* **79**, 755-767.

Yano, A., Ogura, M., Sato, A., Sakaki, Y., Shimizu, Y., Baba, N. and Nagasawa, K. (1997). Effect of modified magnetic field on the ocean migration of maturing chum salmon, *Oncorhynchus keta*. *Mar. Biol.* **129**, 523-530.

Zupanc, G. K. H. (2010). *Behavioral Neurobiology: an Integrative Approach*. New York: Oxford University Press.