Geomagnetic imprinting: A unifying hypothesis of long-distance natal homing in salmon and sea turtles

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Several marine animals, including salmon and sea turtles, disperse across vast expanses of ocean before returning as adults to their natal areas to reproduce. How animals accomplish such feats of natal homing has remained an enduring mystery. Salmon are known to use chemical cues to identify their home rivers at the end of spawning migrations. Such cues, however, do not extend far enough into the ocean to guide migratory movements that begin in open-sea locations hundreds or thousands of kilometers away. Similarly, how sea turtles reach their nesting areas from distant sites is unknown. However, both salmon and sea turtles detect the magnetic field of the Earth and use it as a directional cue. In addition, sea turtles derive positional information from two magnetic elements (inclination angle and intensity) that vary predictably across the globe and endow different geographic areas with unique magnetic signatures. Here we propose that salmon and sea turtles imprint on the magnetic field of their natal areas and later use this information to direct natal homing. This novel hypothesis provides the first plausible explanation for how marine animals can navigate to natal areas from distant oceanic locations. The hypothesis appears to be compatible with present and recent rates of field change (secular variation); one implication, however, is that unusually rapid changes in the Earth's field, as occasionally occur during geomagnetic polarity reversals, may affect ecological processes by disrupting natal homing, resulting in widespread colonization events and changes in population structure.

migration | navigation | magnetic | magnetoreception | fish

Animals that migrate long distances have evolved the ability to exploit disparate, widely separated habitats at different times of their lives. In the framework of movement ecology proposed by Nathan *et al.* (1), long-distance migrants integrate external and internal factors, motion capacity, and navigation capacity to produce their final movement paths; these in turn confer advantages such as access to distant food sources, escape from adverse seasonal conditions, and avoidance of predation at vulnerable life history stages. Because equally desirable areas seldom lie in all directions simultaneously, the navigational capacity of long-distance migrants usually includes the ability to direct movement in response to external factors, thus ensuring arrival at appropriate destinations.

From a navigational perspective, some of the most remarkable migrations are accomplished by marine animals that begin life in particular geographic areas, migrate across vast expanses of sea, and then return as adults to their natal areas to reproduce (2, 3). How such animals navigate back to natal areas across seemingly featureless ocean, and after absences ranging in duration from a few years to a decade or more, has remained enigmatic. In this article we propose a new, unifying hypothesis to explain natal homing in two iconic long-distance migrants, salmon and sea turtles. Specifically, we propose that these animals imprint on the magnetic field that exists at their natal area and use this information to return to their natal region years later, close enough for local cues (olfactory in salmon, unknown in sea turtles) to guide them more precisely to their spawning or nesting sites. This magnetic imprinting hypothesis, which focuses on the movement ecology linkage between an environmental factor (the Earth's magnetic field) and navigational capacity, also suggests the surprising possibility that rapid, naturally occurring changes in the Earth's field occasionally exert a strong influence on ecological processes by altering animal movements.

Migrations of Salmon and Sea Turtles

Tremendous variation exists in the life history and migratory patterns of different species and populations of both salmon and sea turtles (4–6). For our purposes, we will focus on those representatives of each group that undergo the longest open-sea migrations, while recognizing that no general description of such complex groups accurately portrays all members (and indeed, that some nonmigratory species and populations exist in each case).

The salmon of interest for our discussion are those that enter the sea and disperse across hundreds or thousands of kilometers of offshore waters before returning several years later to their natal tributaries to spawn (2, 4). In the Pacific northwest, this description applies to some populations of sockeye salmon (*Oncorhynchus nerka*), chinook salmon (*Oncorhynchus tshawytscha*), and chum salmon (*Oncorhynchus keta*), among others. Natal homing is very precise in that the vast majority of these fish return to their river of origin and often to a particular river branch (4, 7).

The turtles of interest leave their natal beaches as hatchlings, migrate to the open sea, and spend a period of years in distant oceanic and/or neritic areas before eventually returning to the natal region to reproduce. In some cases, such as in certain populations of loggerhead turtles (*Caretta caretta*), young turtles follow complex migratory pathways that lead across entire ocean basins and back; in other species, such as the Kemp's ridley turtle (*Lepidochelys kempii*) and the green turtle (*Chelonia mydas*), the oceanic phase may involve movements that are shorter but which nevertheless take the turtles hundreds or thousands of kilometers from their natal beaches (8, 9). Genetic analyses have indicated that the precision of natal homing may vary considerably among different populations and species; homing to regions of coastline several hundred km in length is common, although greater or poorer precision may exist in some cases (10–14).

Biphasic Navigation

A striking similarity between salmon and sea turtles is that both have been hypothesized to complete long-distance reproductive migrations using navigational systems comprised of two different suites of mechanisms which function sequentially over different spatial scales (4, 15). The first system is thought to guide animals

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across large expanses of ocean into the general vicinity of the target area, at which point the second supplants the first and guides the animals more precisely to the final goal.

For salmon, olfactory cues are of primary importance in guiding the fish to their spawning grounds once they arrive in the vicinity of their target rivers and begin to migrate upstream (16–20). That salmon imprint on the chemical cues of their natal rivers and streams 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., 18–20).

Under favorable conditions (for example, in fjords or other sheltered areas with limited vertical mixing), chemical cues from rivers might extend a considerable distance from a river mouth (17). However, such cues cannot persist and extend across more than a thousand kilometers of ocean, the distance over which some populations of salmon are known to migrate (2, 18). For this reason, salmon navigation in the open sea is thought to involve a different set of mechanisms that are not olfactory (e.g., 4, 18, 21). How salmon navigate from the open ocean into the vicinity of the correct river mouth, however, has never been explained.

For sea turtles, the situation that exists in salmon is essentially reversed, in that little is known about the local cues used by turtles to pinpoint nesting areas once they have drawn near. Directed movements over long distances and into the vicinity of nesting areas, however, can plausibly be explained by the known ability of turtles to exploit variations in the Earth's magnetic field as a kind of magnetic positioning system or "magnetic map" (22, 23). To explore the implications of magnetic navigation for natal homing, we will begin by briefly summarizing important aspects of the Earth's magnetic field.

Positional Information in the Earth's Field

The Earth's magnetic field resembles the dipole field of a giant bar magnet (Fig. 1). Field lines leave the southern hemisphere and curve around the globe before reentering the planet in the northern hemisphere. Several geomagnetic elements vary predictably across the surface of the Earth (Fig. 1). For example, at each location on the globe, the magnetic field lines intersect the Earth's surface at a specific angle of inclination. At the magnetic equator, the field lines are parallel to the ground and the inclination angle is said to be 0°. The field lines become progressively steeper as one moves toward the magnetic poles; at the poles themselves, the field lines are perpendicular to the Earth's surface. Thus, inclination angle varies predictably with latitude, and an animal able to detect this field element may be able to determine whether it is north or south of a particular area.

In addition to inclination angle, three other magnetic field elements related to intensity (i.e., the intensity of the total field, horizontal field, and vertical field) vary across the Earth's surface in ways that make them suitable for use in position-finding (3, 24) (Fig. 1). For animals that can perceive the direction of true geographic north (for example, by using star patterns to determine the axis of Earth's rotation), additional magnetic parameters such as declination (the difference between true north and magnetic north) are also potential cues.

Magnetic Cues as Markers of Coastal Regions

The rivers that serve as major spawning grounds for salmon meet the sea along continental coastlines or along the coasts of large islands such as those of Japan. Similarly, most major sea turtle rookeries are located on continental coastlines (e.g., Mexico, Costa Rica, the southeastern United States, Africa, and Australia). Thus, during reproductive migrations, the essence of the open-sea navigational task that most salmon and sea turtles confront is to travel to a distant coastal area, close enough to the target that other local cues can be used to pinpoint the final destination.

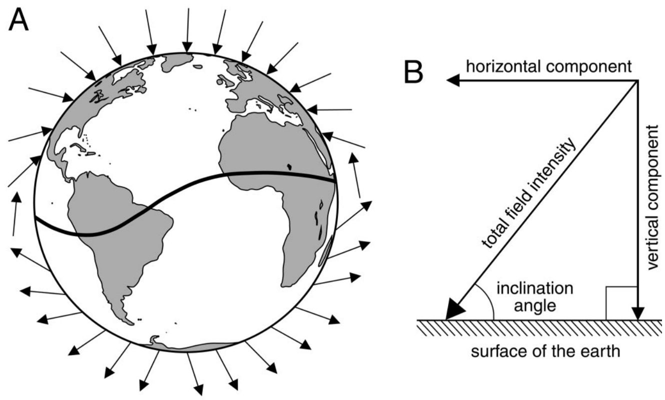

Fig. 1. The Earth's magnetic field. (*A*) Diagram illustrating how field lines (represented by arrows) intersect the Earth's surface and how inclination angle (the angle formed between the field lines and the Earth) varies with latitude. At the magnetic equator (the curving line across the Earth), field lines are parallel to the Earth's surface. The field lines become progressively steeper as one travels north toward the magnetic pole, where the field lines are directed straight down into the Earth and the inclination angle is 90°. (*B*) Diagram illustrating four elements of geomagnetic field vectors that might, in principle, provide turtles with positional information. The field present at each location on Earth can be described in terms of total field intensity and inclination angle. The total intensity of the field can be resolved into two vector components, the horizontal field intensity and the vertical field intensity. (Whether animals can resolve the total field into vector components is not known.)

How, then, might an animal in the open ocean arrive reliably at a particular region of coastline from a considerable distance away? An interesting possibility is that geomagnetic parameters can be used to identify particular coastal areas. The west coast of North America illustrates the basic principle (Fig. 2). The coastline is aligned approximately north-south, whereas the isolines of inclination trend east-west. As a consequence, every area of coastline is marked by a different inclination angle (Fig. 2*A*). Similarly, isolines of total field intensity run approximately east-west in this geographic area and different coastal locations are thus marked by different intensities (Fig. 2*B*). In effect, different coastal areas have unique "magnetic signatures" that might, in principle, be used to identify a natal region and distinguish it from all other locations along the same coast. The same is true along the east coast of North America and, indeed, along most continental coastlines worldwide.

Geomagnetic Imprinting Hypothesis

Given that different areas along continental coastlines are marked by distinctive magnetic fields, one possibility is that both salmon and sea turtles imprint on the magnetic signatures of their natal areas and use this information years later to direct natal homing. Although many variants of the hypothesis are possible, the simplest involves imprinting on a single element of the field (e.g., either inclination angle or intensity). To locate the area later in life, the animal would need only to find the coastline, and then swim north or south along it to reach the target region.

For example, if salmon imprint on the magnetic inclination angle that exists at a river mouth when they first enter the ocean, then a fish seeking its natal river several years later could hypothetically find the coastline and swim along it until the appropriate inclination angle is encountered. The initial process of locating the coastline might be facilitated if fish in the open sea begin their spawning migration by swimming in a particular

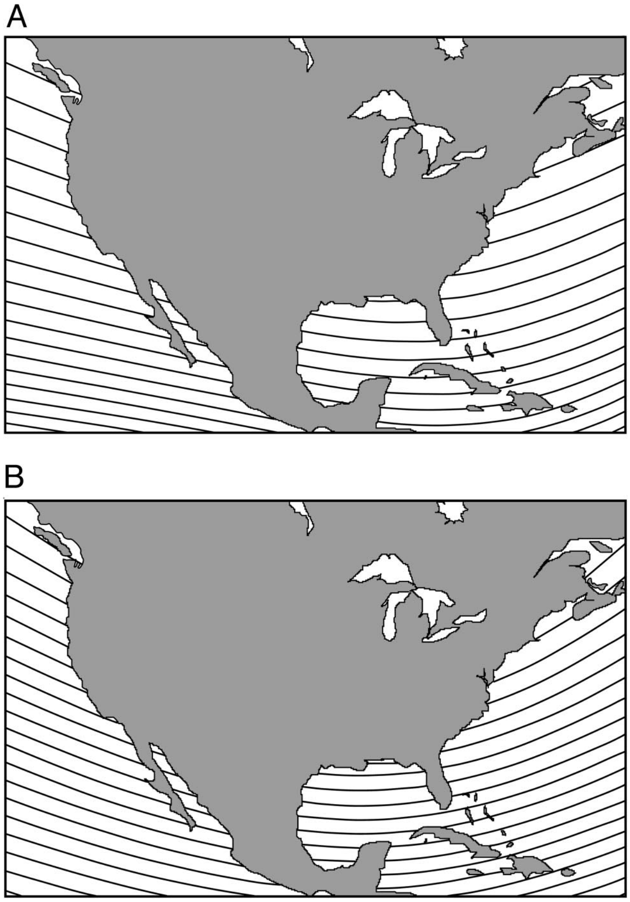

Fig. 2. Isolines of magnetic field elements along the coasts of North America derived from the World Magnetic Model for the year 2005. (*A*) Isoclinics (isolines of magnetic field inclination). Each region of the west coast is marked by a different inclination angle; a similar situation exists for the east coast. Adjacent isoclinics represent differences in inclination of 2°. (*B*) Isodynamics (isolines of total field intensity). Adjacent isolines represent differences in intensity of 1,000 nT.

compass direction (e.g., east); such a directional preference might be inherited or perhaps learned as a reversal of the direction that the fish traveled early in life while moving downriver or out to sea. Still another possibility is that salmon, turtles, or both might adjust position in the open ocean until they arrive at the correct isoline and then move along it toward the coast and the natal area.

More complex strategies of magnetic imprinting, and of magnetic navigation, are also hypothetically possible. For example, a salmon might imprint on both inclination and intensity, and use both elements as redundant markers of the natal area upon return. The demonstrated ability of sea turtles to detect inclination and intensity (see below) has fueled speculation that turtles might navigate using a bicoordinate magnetic map in at least some oceanic regions where the alignment of inclination and intensity isolines are favorable (3, 22). Regardless, however, bicoordinate magnetic navigation does not need to be invoked for geomagnetic imprinting to occur along continental coastlines because the coast in effect functions as one fixed coordinate.

It is important to emphasize again that the hypothesis of geomagnetic imprinting pertains only to the initial, long-distance phase of natal homing migrations. It seeks to explain how salmon and sea turtles arrive in the general region of their natal areas, but is not intended to account for the second and more precise task of pinpointing specific spawning and nesting areas, a step

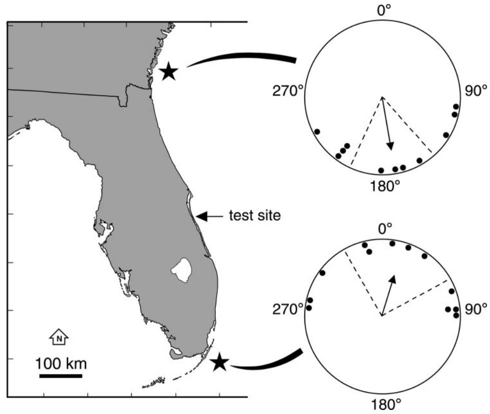

Fig. 3. Evidence for a magnetic map in juvenile green turtles. Juvenile turtles were captured in feeding grounds near the test site in Melbourne Beach, FL. Each turtle was exposed to a magnetic field that exists at one of two distant locations (represented by stars along the coastline). Turtles exposed to the field from the northern site swam approximately southward, whereas those exposed to the field from the southern site swam approximately north. 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 is modified from ref. 23. See text for details.

assumed to be achieved using nonmagnetic local cues (21). For salmon, the hypothesis is therefore not in conflict with olfactory imprinting or the established role of olfactory cues in guiding fish upriver. The hypothesis proposes instead that a second type of imprinting occurs in tandem with olfactory imprinting and functions in guiding long-distance movements that precede the part of the migration guided by olfactory cues.

Detection of Magnetic Parameters

Can salmon and sea turtles detect the magnetic parameters necessary for geomagnetic imprinting? Sea turtles evidently can; experiments have demonstrated that hatchling loggerhead turtles perceive both magnetic inclination angle (25) and magnetic field intensity (26). Furthermore, when hatchlings were subjected to magnetic fields that exist at three widely separated locations along their open-sea migratory pathway, they responded by swimming in directions that would, in each case, facilitate movement along the migratory route (27). These results imply that turtles can distinguish among magnetic fields that exist in different geographic locations.

Additional work has demonstrated that older turtles are able to use magnetic positional information to facilitate navigation toward specific geographic goals along coastlines (22, 23). Juvenile green turtles captured in feeding grounds along the east coast of Florida were tethered to a tracking system inside a pool of water on land and exposed to magnetic fields that exist at locations ≈340 km north or south of the capture site (23). Turtles exposed to the field from the northern area swam south, whereas those exposed to the field from the southern location swam north (Fig. 3). Thus, turtles swam in directions that would have led them home had they actually been displaced to the locations where the two fields exist. These results imply that well before the turtles mature they have already acquired a magnetic map and the skills needed to navigate toward specific coastal areas.

In comparison to turtles, little is known about the magnetic sensing abilities of salmon. Young salmon are capable of orienting to the Earth's field (28, 29), a finding which demonstrates, at a minimum, that they have a magnetic compass capable of guiding them in specific directions such as north and south. Crystals of magnetite that might function as receptors for the magnetic sense have been discovered in salmon and closely

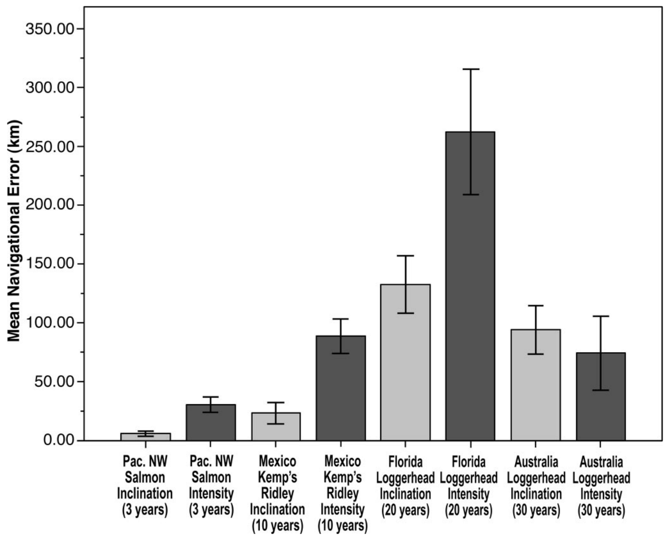

Fig. 4. Navigational errors that would hypothetically accrue due to secular variation, assuming various absences, geographic locations, and strategies of geomagnetic imprinting (see text). Animals were assumed to be unable to detect or compensate for secular variation; they were also assumed to be absent from the natal region until reproductive maturity. Analyses were done for four different situations: (*i*) salmon leaving the Columbia River in Washington state and returning after 3 years; (*ii*) Kemp's ridley turtles leaving their nesting beach at Rancho Nuevo, Mexico, and returning after 10 years; (*iii*) loggerhead turtles leaving Melbourne Beach, FL, and returning after 20 years; (*iv*) loggerhead turtles leaving Mon Repos, Queensland, Australia, and returning after 30 years. In each case, the measurements reported indicate the distance by which an adult animal would miss its natal site if it were to return to the coastal location which has the same magnetic inclination or intensity that marked the natal site at the time the animal departed. Measurements represent means of repeated simulations at 5-year intervals from 1900 to the present. In other words, the salmon simulation involved a fish leaving the coast in 1900 and returning in 1903, a second fish leaving the coast in 1905 and returning in 1908, a third fish leaving in 1910 and returning in 1913, and so on. Error bars represent 95% confidence intervals of the mean.

related fish (30, 31). The possibility that salmon can also detect elements of the field such as inclination and intensity, and use this information to assess their position in the open sea, has been discussed (31, 32); at present, however, no experimental evidence supports the hypothesis.

Geomagnetic Imprinting and Secular Variation

The Earth's magnetic field and its constituent elements (such as inclination and intensity) change gradually over time (24). This change in field elements, known as secular variation, poses a potential complication for the geomagnetic imprinting hypothesis because field changes that occur at the natal site during an animal's absence might cause navigational errors during return migrations (3).

Quantifying navigational errors that might occur due to secular variation is difficult for several reasons. For instance, the rate of field change varies among different geographic regions and at different points in time; thus, no typical worldwide value exists. Several simple modeling exercises, however, imply that geomagnetic imprinting is compatible with present and recent rates of secular variation. For example, species of salmon such as coho, sockeye, and chinook that reproduce in tributaries of the Columbia River in Washington state typically return to the river after ≈3 years at sea (2, 33). Analyses indicate that navigational errors of returning salmon would have averaged ≈6 km over the past century if the fish imprinted on the inclination angle at the mouth of the Columbia River and ≈31 km if they imprinted on total intensity (Fig. 4).

The situation in sea turtles is more complex, inasmuch as different populations and species of turtles reach maturity at very different ages. For example, Kemp's ridley turtles (*L. kempii*) are thought to mature in as little as a decade (34), whereas loggerhead turtles in some areas require as much as 30 years (35).

An analysis of navigational errors that would hypothetically 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 (Fig. 4). For example, at beaches of eastern Mexico where Kemp's ridley turtles nest, a strategy of returning to a coastal area marked by a specific inclination angle would presumably be effective, inasmuch as the isoclinic (inclination isoline) seldom drifts more than a few kilometers away during a year. A turtle imprinting on inclination and returning after a decade would, on average, arrive ≈23 km from its natal site.

Relative to eastern Mexico, the rate of field change is faster in Melbourne Beach, FL (one of the largest nesting areas for loggerhead turtles in the Atlantic), but slower in Mon Repos, Australia (the largest nesting area for Australian loggerheads). Turtles in the Florida population take ≈20 years to mature (36); given rates of secular variation during the past century, these turtles could hypothetically return a mean distance of ≈134 km from their natal site if they imprinted on inclination angle, or ≈262 km from it if they used intensity. Although such displacements seem large, they are not incompatible with the regional homing demonstrated for this population (37), or with the tendency of some Florida loggerheads to deposit different nests in widely separated areas that span >200 km of coastline (38). In Mon Repos, Australia, the time to maturity is longer than that of Florida loggerheads (≈30 years vs. 20, ref. 35) but the rate of field change during the past century has been slower. As a result, an absence of 30 years would hypothetically result in average errors of ≈94 km if the turtles imprinted on inclination or 74 km if they imprinted on intensity.

As these examples illustrate, the field changes that are presently occurring along continental coasts where salmon spawn and sea turtles nest are, at least in the cases studied, not enough to prevent animals from returning to their natal regions, close enough to the target area for local cues to plausibly guide migrants to their final destinations. Although the geomagnetic imprinting hypothesis is clearly most appealing for salmon and other animals that are gone from the natal site for relatively short periods of time, it is plausible even for turtles absent for a decade or more.

Natal Homing by Juvenile Turtles

A relatively recent finding is that natal homing on regional scales occurs not only in adult turtles returning to nest, but also in juveniles of at least one species. After a period of years in the open ocean, juvenile sea turtles of several species take up residence in neritic feeding grounds (8). When juvenile loggerheads transition to this phase of their life cycle, they choose foraging grounds within their general natal region more often than would be expected by chance (11, 39). The precision of this juvenile natal homing, and the mechanisms that underlie it, have not yet been determined.

The regional homing of juvenile turtles raises the interesting possibility that such animals may be able to 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. If so, then navigational errors attributable to secular variation might be significantly smaller for turtles than the estimates we have presented in Fig. 4.

Island-Nesting Turtles

Although nearly all major sea turtle rookeries are located along continental coastlines, some populations, often of relatively small size, nest on islands. Island-nesting populations are thought to be derived evolutionarily from populations that nest on continents (11), but whether the two groups locate their natal regions in the same way is not known. It is possible, for example, that different strategies of navigation and imprinting evolved as an adaptation for island nesting, or that different populations vary depending on what is effective in a given geographic setting (21).

In principle, finding an island is possible using a single magnetic element such as inclination or intensity (21). Thus, a magnetic imprinting process 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 bicoordinate magnetic navigation to return, might also be feasible in some situations (3, 21). Experimental evidence indicates that adult turtles use magnetic cues when navigating to islands, although in what exact way is not known (40).

At present, insufficient information exists to make a meaningful assessment of the navigational errors that might arise from secular variation if turtles that nest on islands rely on magnetic imprinting. Little is known, for example, about how long turtles in such populations take to mature, or whether they return to the natal region (at least temporarily) as juveniles; the outcome of calculations is strongly affected by assumptions about these matters, as well as by the geographic region of interest and the precise navigational strategy that turtles are assumed to use (whether, for example, they use a single magnetic element or a bicoordinate magnetic map). These areas may prove fruitful for future inquiry.

Why Did Natal Homing Evolve?

Regardless of how it is accomplished, navigating hundreds or thousands of kilometers to reproduce in a particular geographic area does not appear to be advantageous when other suitable sites for reproduction often exist along the way. The costs of such migrations appear considerable in terms of energy expenditure, stress, and risk. For such a pattern to evolve, the benefits must be correspondingly high. In evolutionary terms, natal homing presumably arose because individuals that returned to their natal areas to reproduce had greater success than those that tried to reproduce elsewhere.

In all likelihood, the structure of the environment has been a major factor in shaping natal homing in sea turtles and salmon, inasmuch as successful reproduction for each requires a specialized set of environmental conditions that exist only in limited and highly specific geographic areas (3, 4). For sea turtles, the need to lay eggs on land restricts possible nesting locations to a tiny fraction of the environment in which the animals live. Indeed, even most coastal areas are unsatisfactory because the beach must consist of sand rather than rock or mud and the sand must possess specific qualities favorable for nest construction. In addition, the beach must be free of steep inclines and obstacles that block access from the sea; it must have suitable incubation temperatures, low densities of egg predators, and close proximity to ocean currents that can help transport hatchlings to suitable developmental habitats. For salmon, the need to spawn in fresh water similarly restricts reproduction to rivers and streams that can be readily reached from the ocean and are not blocked by large waterfalls or other barriers; in addition, spawning areas must have appropriate depths, temperature, flow conditions, and a substrate such as gravel that will facilitate retention of developing embryos.

To human observers, an irrational feature of natal homing is that animals often forego reproducing in suitable nearby areas to migrate long distances to their natal sites. For example, some sea turtles feed in areas adjacent to nesting beaches used by their own species, but nevertheless migrate long distances to nest elsewhere (41); similarly, salmon on their way to their own natal rivers often swim past other rivers where large populations of conspecifics spawn (4). From the perspective of the animal, however, assessing the suitability of an unfamiliar area for reproduction may be very difficult. A turtle crawling out of the sea to nest probably cannot tell that a large population of raccoons is nearby and will consume her eggs after she departs, and salmon passing by the mouth of an unfamiliar river may be unable to determine whether there are suitable spawning grounds a hundred kilometers upstream, or instead an impassable waterfall.

Under such conditions, in which suitable reproductive habitat is scarce and reproductive output can be strongly affected by factors that are difficult to assess, it is perhaps not surprising that natural selection has favored individuals that return to their natal areas to reproduce. In effect, the very existence of an adult animal confirms that its natal area has the attributes needed for successful reproduction, an assurance that no other location can provide.

Navigational Errors and Colonization Events

Once it arises, natal homing has important implications for population structure. If mating is restricted to natal areas, then gene flow among populations that home to different locations is restricted and reproductive isolation can occur. In salmon, isolated populations in different rivers have been subjected for many generations to slightly different physical and biotic factors and have evolved specializations that enhance survival in the home river (42, 43). Such adaptations may in turn reinforce the benefits of natal homing, inasmuch as fish that return to their home streams will be better adapted to their natal sites than to other areas, and strays will also be less successful than the local fish.

Although salmon and turtles both display strong tendencies toward natal homing, it is important to recognize that straying also occurs on a regular basis. In salmon, tagging studies have demonstrated that a small percentage of fish fail to return to their home rivers each year and are instead recaptured in other streams and rivers, usually but not always nearby (44, 45). Comparable studies have not been done with sea turtles, but, in many instances, turtles evidently home to natal regions rather than to highly specific nesting sites (11). The absence of precise natal homing in many turtle populations, or at least the willingness to select nest sites over a considerable expanse of coastline, may be adaptive because particular nesting areas can be destroyed rapidly by storms, erosion, and flooding.

From an ecological perspective, straying from natal areas is crucial because without it, new habitat would never be colonized. For salmon, Quinn (32) has hypothesized that straying and homing are under genetic control and are maintained in dynamic equilibrium within species and populations. According to this reasoning, natural selection will favor precise homing in areas where spawning sites are of consistently high quality year after year. In areas where the quality of spawning sites varies greatly in different years, however, natural selection should favor females which produce some offspring that home and others that stray; this strategy maximizes the likelihood that at least some progeny will encounter favorable areas when they return to reproduce.

An interesting possibility is that individuals that stray might do so because they have deficiencies in imprinting, navigational systems, or both, and are thus unable to relocate their natal sites. Alternatively, strays might be able to home normally but, for whatever reason, choose to reproduce elsewhere. Either way, for strays to found enduring new populations, at least some of their offspring must presumably be capable of returning to the new home area.

If the geomagnetic imprinting hypothesis is correct, an intriguing speculation is that unusually rapid changes in the Earth's magnetic field, as are thought to have occurred on rare occasions during some magnetic polarity reversals (46, 47), might temporarily disrupt natal homing on a massive scale. This in turn might lead to considerable ecological upheaval, as mass straying brings formerly isolated populations into contact and animals unable to locate their natal sites discover and colonize new areas (which subsequent generations can locate reliably as the field stabilizes and natal homing once more becomes possible).

For now, only time and careful experimentation will reveal whether geomagnetic imprinting is indeed the centerpiece of long-distance natal homing in salmon and sea turtles, and whether the Earth's magnetic field does indeed play an indirect and previously overlooked role in maintaining population structure in some species. In the meantime, the navigational capacity of animals that guide themselves across vast expanses of seemingly featureless ocean, and the interaction of navigation with other elements of the movement ecology model (1, 48), remain fertile areas for inquiry.

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