

Review

The sensory ecology of ocean navigation

Kenneth J. Lohmann*, Catherine M. F. Lohmann and Courtney S. Endres

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

*Author for correspondence (e-mail: klohmann@email.unc.edu)

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Summary

How animals guide themselves across vast expanses of open ocean, sometimes to specific geographic areas, has remained an enduring mystery of behavioral biology. In this review we briefly contrast underwater oceanic navigation with terrestrial navigation and summarize the advantages and constraints of different approaches used to analyze animal navigation in the sea. In addition, we highlight studies and techniques that have begun to unravel the sensory cues that underlie navigation in sea turtles, salmon and other ocean migrants. Environmental signals of importance include geomagnetic, chemical and hydrodynamic cues, perhaps supplemented in some cases by celestial cues or other sources of information that remain to be discovered. An interesting similarity between sea turtles and salmon is that both have been hypothesized to complete long-distance reproductive migrations using navigational systems composed of two different suites of mechanisms that function sequentially over different spatial scales. The basic organization of navigation in these two groups of animals may be functionally similar, and perhaps also representative of other long-distance ocean navigators.

Key words: navigation, orientation, migration, magnetic, hydrodynamic, chemical, olfactory, sea turtle, fish, whale, salmon.

Introduction

Considerable progress has been made in characterizing the mechanisms of orientation and navigation used by diverse animals. Most work has focused on terrestrial groups such as insects and birds, which are readily accessible and provide favorable subjects for studies both in the field and in the laboratory (reviewed by Wiltschko and Wiltschko, 1995; Wiltschko and Wiltschko, 2003; Wehner et al., 1996; Wehner, 1998; Åkesson and Hedenström, 2007). Significantly less is known, however, about how animals guide themselves over the 70% of the Earth's surface that is covered by ocean.

Animals that migrate long distances through the sea, and especially pelagic species like sea turtles and cetaceans that travel across deep water, inhabit a sensory environment fundamentally different from that of the terrestrial world. Below the air-sea interface light diminishes rapidly with depth. The light field is transformed by absorption, scattering, refraction and the constant movement of waves across the ocean surface. Visual landmarks are absent and, except in unusually clear and calm water immediately below the surface, celestial cues such as the position of the sun and stars cannot be perceived.

At the same time, the marine environment provides animals with numerous potential cues that do not exist on land. In many oceanic regions, waves driven by steady winds propagate through the sea in seasonally constant directions (Hogben and Lumb, 1967; Lohmann, 1992). Water pressure can convey information about depth (Fraser and Macdonald, 1994). Distinctive chemical cues emanating from estuaries provide salmon (Dittman and Quinn, 1996), and perhaps other animals, with markers of ecologically important locations. Sound and electrical currents travel more readily through the sea than through air, and some marine animals are adept at detecting each (Harley et al., 2003; Kalmijn, 1971). Clearly,

animals navigating through the ocean have access to a suite of navigational cues which differs from that of their terrestrial counterparts.

A second difference between the terrestrial and open-ocean environment lies in the degree to which animals can control their paths. Caribou migrating across tundra, or insects crawling across the ground, can be reasonably assured of moving in the same direction in which they walk. Even birds, which can be blown off course by winds while migrating, can often mitigate drift by maintaining visual contact with the ground and by landing when conditions are adverse (Richardson, 1991; Erni et al., 2002). Circumstances differ for pelagic migrants. In the open sea, the movements of animals are continuously susceptible to the influence of currents; animals also lack stationary visual references against which drift can be gauged and cannot opt out by grounding themselves.

This difference in the ability of terrestrial and pelagic animals to control their paths has significant implications for navigation. On land, some navigational strategies depend on an expectation that the direction and distance traveled approximately reflect the direction and duration of an animal's attempted movements; examples include the path integration of desert ants (Wehner et al., 1996) and the clock-and-compass orientation that guides many young birds during their first migration (Wiltschko and Wiltschko, 2003). Such strategies are unlikely to be successful for migrants in the open ocean, where swimming movements are permanently uncoupled from solid substrate. For pelagic migrants traveling long distances to specific target areas, navigational systems must therefore accommodate continuous drift and correct for errors that will inevitably arise.

Although the study of long-distance navigation in ocean animals is still at an early stage, research has begun to provide insight into

how a few species maintain consistent headings through the ocean and navigate to specific target areas. In this paper we highlight recent advances and emerging principles. Our examples are selective rather than exhaustive, and we focus primarily on sea turtles and salmon, two iconic long-distance ocean migrants whose navigational systems have been the subject of considerable study and speculation. We begin by briefly reviewing methods for studying ocean navigation, highlight three sets of environmental cues that ocean migrants are known to use, and conclude by suggesting that long-distance navigation in the sea is often (and perhaps always) accomplished through the sequential use of different suites of guidance mechanisms that operate over different spatial scales.

Studying ocean navigation

Three basic approaches can be used to study the navigation of ocean animals. First, behavioral studies can be conducted in the lab. Second, experiments can be carried out in the ocean. Finally, migratory routes can be analyzed for insight into navigational processes. Each of these approaches has a different set of advantages and limitations.

Laboratory experiments provide an opportunity to test hypotheses under controlled conditions in which one variable at a time can be manipulated. This approach has been particularly powerful in demonstrating the existence of various guidance mechanisms and has been used successfully with hatchling sea turtles (e.g. Lohmann and Lohmann, 1996a; Lohmann and Lohmann, 2003), immature fish (e.g. Quinn, 1980; Quinn and Brannon, 1982), invertebrates (Rudloe and Herrnkind, 1980; Boles and Lohmann, 2003), and other small animals. One limitation is that such experiments do not always reveal the circumstances under which each mechanism is used in nature. For example, showing that an animal has a magnetic compass does not by itself indicate where and when this ability is used.

Under favorable conditions, experiments conducted in the ocean can reveal which sensory cues are used and when (e.g. Lohmann and Lohmann, 1992; Luschi et al., 2007). An important caveat, however, is that numerous sources of directional and positional information are always simultaneously present in the sea and many animals switch among these when the need arises (Able, 1993). Thus, interpreting the results of field experiments can often be difficult. For example, if covering the eyes of a migrating animal does not cause it to change course, this does not necessarily imply that visual cues are not used; it might mean only that alternative cues were available under the test conditions.

The third method involves analyzing the tracks of animals. Satellite telemetry has provided hundreds of tracks of marine animals migrating long distances (e.g. Nichols et al., 2000; Le Boeuf et al., 2000; Bonfil et al., 2005), and various attempts have been made to relate such tracks to specific oceanographic, geophysical and topographic features. Unfortunately, knowing the track of an animal is not the same as knowing how the animal navigates; correlations alone are insufficient to demonstrate the involvement of any particular cue (Fig. 1). Nevertheless, careful analyses of tracks can sometimes provide ideas about potential navigational strategies that have not previously been considered (e.g. Alerstam et al., 2001).

Compasses, maps and navigation

The minimal information needed by an animal to guide itself through the sea depends largely on the nature and duration of the movement, the complexity of the route, and whether there is a specific goal that the animal is trying to reach. In some cases, orientation in a constant direction is sufficient. For example, blue crabs scuttling

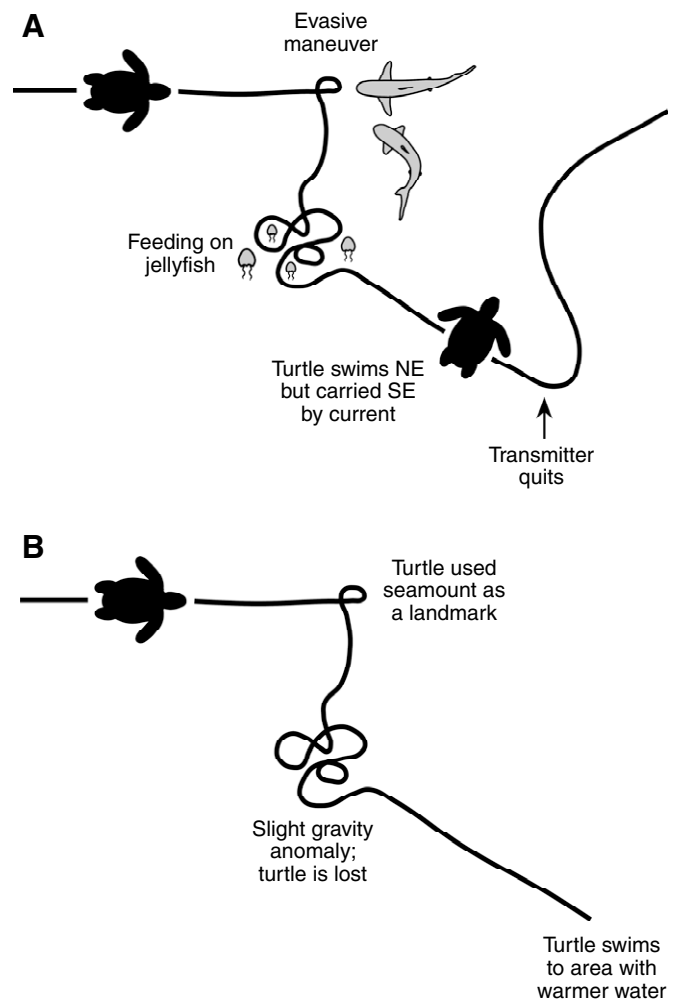


Fig. 1. Diagram illustrating potential problems in attempting to infer mechanisms of navigation from the tracks of animals. (A) Overhead view of the track of a hypothetical sea turtle moving hundreds of kilometers through the ocean and monitored with satellite telemetry; events that occurred along the way are indicated. (B) A plausible but erroneous interpretation of the turtle's path. In this hypothetical example, researchers unaware of what happened in the ocean superimposed the track on several topographical and geophysical maps until correlations were found between changes in the turtle's behavior and specific features of the environment. These environmental cues were then assumed to have elicited the behavioral changes, leading to incorrect inferences about navigational mechanisms.

from shallow water to the safety of deeper areas (Nishimoto and Herrnkind, 1978) and hatchling sea turtles migrating from their natal beaches to deep water (Lohmann and Lohmann, 1996a; Lohmann and Lohmann, 2003) move toward broad, offshore areas rather than toward specific destinations. Under such conditions, all that is needed is a way to maintain a consistent offshore heading.

In contrast, salmon returning from thousands of kilometers away to the mouth of a specific river need more than a simple directional or compass sense. Animals capable of homing to particular locations are often said to possess both a map and a compass. According to this model, the map sense enables the animal to determine its position relative to the goal (or at least the direction in which it should travel), while the compass sense is used to maintain a heading in the appropriate direction (Kramer, 1961; Able, 2001). In principle, other ways also exist to locate distant targets. For example, animals might

search over a large area, or follow simple rules or algorithms that lead them into the vicinity of a goal (e.g. swim west until a coastline is encountered; swim south if the water temperature is cold).

Although numerous sources of directional and positional information are potentially available to long-distance migrants in the sea, recent work has highlighted the importance of three particular types of cue: geomagnetic, chemical and hydrodynamic. These three sources of information, perhaps supplemented in some cases by celestial cues, may provide the fundamental building blocks for much of the navigational repertoire of ocean migrants. We will briefly consider each in turn.

Magnetic maps and compasses

The Earth's magnetic field is a pervasive environmental feature that is present throughout the day and night, remains unaffected by weather and season, and exists in all parts of the ocean, from shallowest to deepest. Animals can evidently extract at least two distinct types of information from the geomagnetic field (Wiltshcko and Wiltshcko, 1995; Johnsen and Lohmann, 2005). The simplest of these is directional or compass information, which enables an animal to maintain a consistent heading in a particular direction such as north or south. The list of marine animals known to possess magnetic compasses includes isopods (Ugolini and Pezzani, 1995), spiny lobsters (Lohmann et al., 1995a), sea turtles (Lohmann, 1991; Lohmann and Lohmann, 1993), rays (Kalmijn, 1978) and salmon (Quinn, 1980; Quinn et al., 1981).

In addition to providing a source of compass information, the Earth's field also provides a potential source of positional or 'map' information (reviewed by Lohmann et al., 2007). Several geomagnetic elements vary in a predictable way across the surface of the Earth and might, in principle, be used to assess geographic location (Fig. 2). For example, at each location on the globe, the magnetic field lines intersect the Earth's surface at a specific inclination angle. At the magnetic equator, the field lines are parallel to the Earth's surface, but become progressively steeper as one moves toward the magnetic poles. 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. Similarly, the intensity of the total field, or the intensity of the horizontal and vertical field components, might also hypothetically be used in position finding. For animals that can perceive the direction of true geographic north (for example, by using star patterns to determine the location of the north pole), still other magnetic parameters such as

declination (the difference between true north and magnetic north) are potentially available.

Hatchling loggerhead turtles (*Caretta caretta*) detect both magnetic inclination angle (Lohmann and Lohmann, 1994) and field intensity (Lohmann and Lohmann, 1996b). 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 (Fig. 3) (Lohmann et al., 2001). These results imply that young turtles have a 'magnetic map' in which regional magnetic fields function as navigational markers and elicit changes in swimming direction at appropriate geographic locations (Lohmann et al., 2007). Moreover, these responses appear to be inherited, inasmuch as the hatchlings tested had never been in the ocean.

Older turtles are apparently able to learn the magnetic topography of the areas in which they live and incorporate this information into magnetic maps that help them navigate toward specific goals (Lohmann et al., 2004; Lohmann et al., 2007). In one experiment, juvenile green turtles (*Chelonia mydas*) were captured in feeding grounds along the Florida coast, placed in an orientation arena, and exposed to magnetic fields that exist at locations approximately 340 km north or south of the capture site (Lohmann et al., 2004). Turtles exposed to the field from the northern area swam south, whereas those exposed to the field from the southern location swam north (Fig. 4). Thus, turtles swam in directions that would have led them home had they actually been displaced to the locations where the two fields exist.

Adult turtles, like hatchlings and juveniles, also use magnetic information while navigating. In one experiment, adult female green turtles were captured as they came ashore to nest on a remote island in the Indian Ocean. Turtles were displaced 100–120 km by boat and released. One group had strong magnets attached to their heads to disrupt the magnetic environment, while a control group carried non-magnetic brass bars. Turtles bearing magnets returned to the island more slowly, and by more convoluted routes (Luschi et al., 2007; Lohmann, 2007). These results imply that adult turtles use a magnetic map, a magnetic compass, or both while navigating to their nesting grounds.

The possibility that salmon and other fish possess magnetic maps has been discussed by several authors including Quinn (Quinn, 1984) and Walker and colleagues (Walker et al., 1997). Walker and colleagues (Walker et al., 1997) conditioned rainbow trout (*Oncorhynchus mykiss*) to respond to magnetic fields imposed on

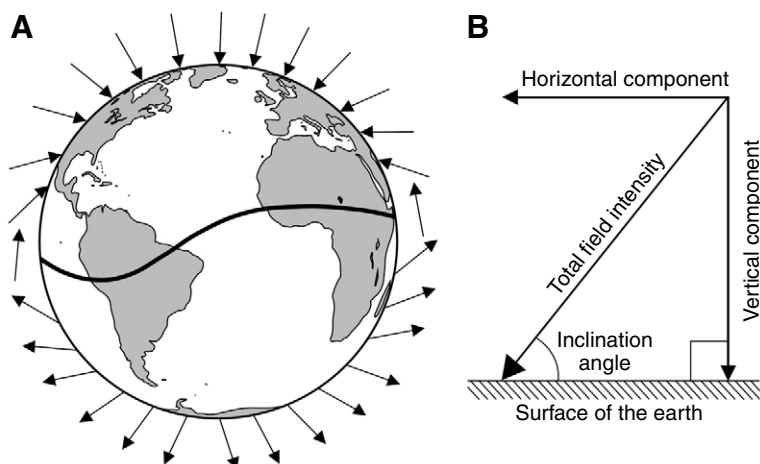


Fig. 2. (A) Diagrammatic representation of the Earth's magnetic field illustrating how field lines (represented by arrows) intersect the Earth's surface, and how inclination angle (the angle formed between the field lines and the Earth) varies with latitude. At the magnetic equator (the curving line 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 a total field intensity and an 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 are able to resolve the total field into vector components is not known.)

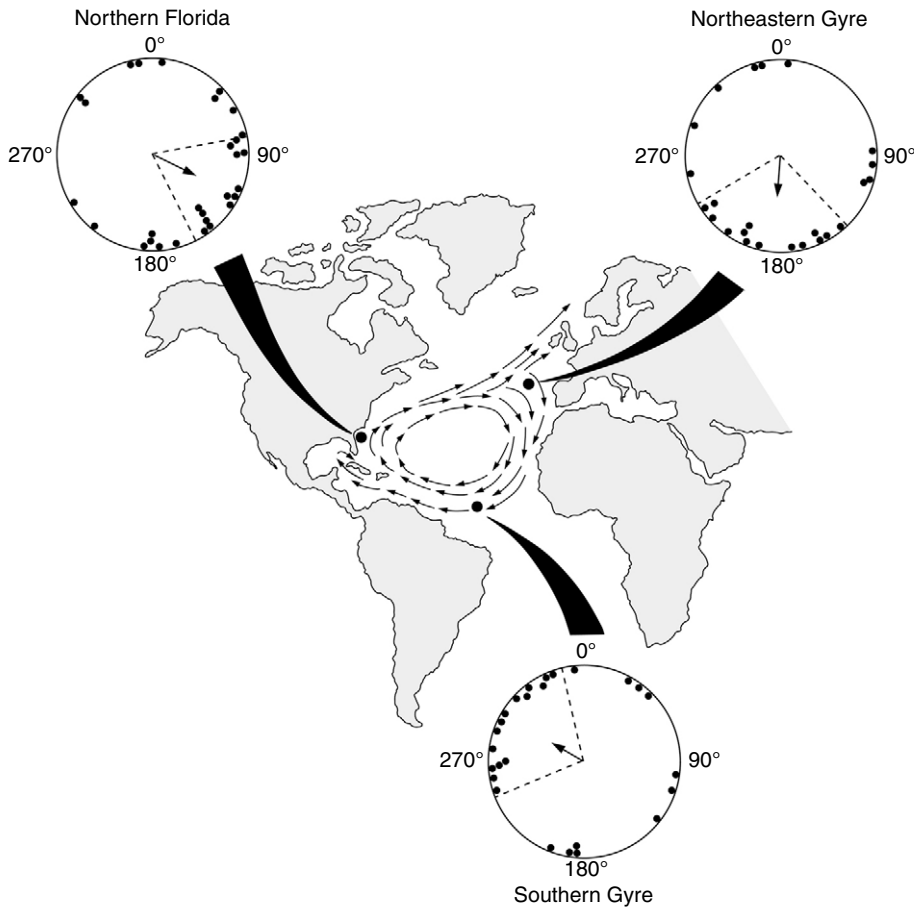


Fig. 3. Orientation of hatchling loggerhead turtles in magnetic fields characteristic of three widely separated locations (marked by black dots on the map) along the migratory route. Generalized main currents of the North Atlantic gyre are represented on the map by arrows. In the orientation diagrams, each dot represents the mean angle of a single hatchling. 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 modified from Lohmann et al. (Lohmann et al., 2001).

them in the laboratory, confirming magnetic sensitivity in this species. However, because the magnetic stimulus altered the intensity, inclination, direction, and gradient of the field simultaneously, the precise element or elements of the field detected by the fish could not be determined.

In a different experiment, four chum salmon (*Oncorhynchus keta*) were tracked as they swam through the sea near the coast of Japan for a period of hours while the magnetic field around them was intermittently disrupted (Yano et al., 1997). No obvious change in orientation behavior was observed when the magnetic field was altered. However, as noted previously (see 'Studying ocean navigation'), interpreting experimental results can be difficult when animals are deprived of one type of cue but are tested in the ocean where numerous alternative cues exist. Although the findings of Yano et al. (Yano et al., 1997) have been interpreted by some as evidence against magnetic maps in salmon (e.g. Døving and Stabell, 2003), others consider the results to be inconclusive (e.g. Walker et al., 2003).

Use of magnetic anomalies?

In some oceanic regions, rocks rich in magnetic minerals produce local magnetic anomalies (Skiles, 1985). Such anomalies are typically small (<1% of the total field at the surface of the ocean) (McElhinny and McFadden, 1999), but in principle might disrupt the field sufficiently to impair the navigation of animals using magnetic maps. On the other hand, the difficulty might be easily solved, given that a fast-moving animal may pass rapidly through such areas just by maintaining a consistent heading for a short time (Lohmann and Lohmann, 1996b; Lohmann et al., 2007).

Although magnetic anomalies have often been viewed as potential problems for magnetically sensitive species (Walcott, 1978), an interesting possibility is that anomalies might sometimes serve as useful markers. For example, many islands and seamounts generate significant anomalies, which might hypothetically provide a useful signal to animals searching for such locations. Interestingly, analysis of hammerhead shark movements near seamounts has led to the suggestion that this species might sometimes follow features of the local magnetic topography (Klimley, 1993).

An unusual pattern of magnetic anomalies exists on the ocean bottom in seafloor-spreading zones (areas where continental plates diverge). As the plates move apart, molten material continually seeps out along the ocean floor and, as it cools, acquires magnetization parallel to the direction of the Earth's field. Because the polarity of the Earth's field has reversed at irregular intervals over geologic time, stripes of ocean floor formed during periods of opposite geomagnetic polarity are magnetized in opposite directions (Skiles, 1985; McElhinny and McFadden, 1999). The magnetic signal of each stripe either adds to the local geomagnetic field, enhancing the total field slightly (creating magnetic maxima), or opposes the present Earth's field (resulting in magnetic minima).

Analyses have suggested that whales tend to be found along these magnetic pathways more often than should occur by chance (Walker et al., 1992) and that whales in some geographic areas tend to become stranded where magnetic minima pathways intersect land (Kirschvink et al., 1986). One interpretation is that whales follow these weak magnetic pathways as they migrate (Kirschvink et al., 1986). If so, the benefits of this strategy relative to other methods

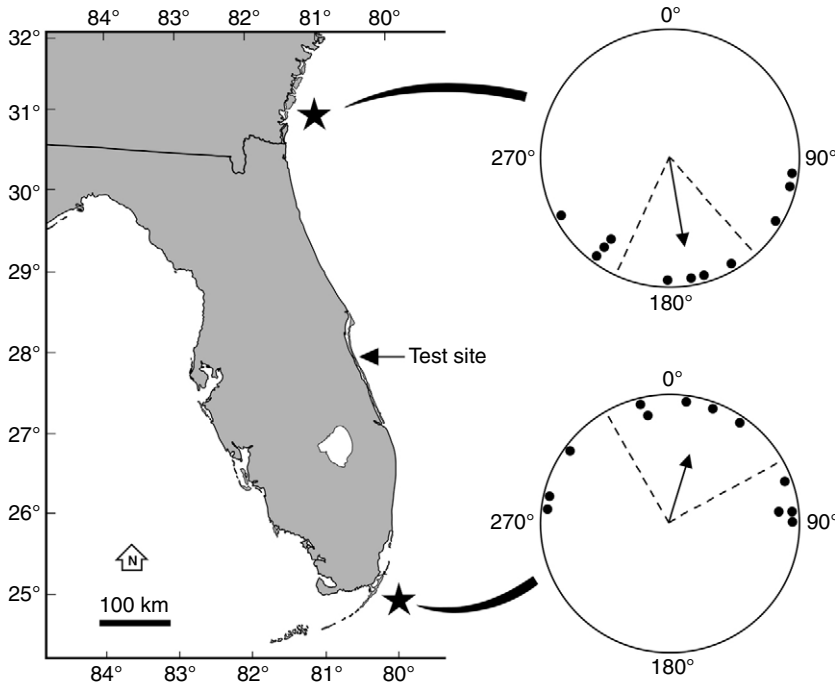


Fig. 4. Evidence for a magnetic map in juvenile green turtles. Juvenile turtles were captured in feeding grounds near the test site in Florida, USA. Each turtle was exposed to a magnetic field that exists at one of two distant locations (represented by stars along the coastline). Turtles exposed to the field from the northern site swam approximately south, 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 modified from Lohmann et al. (Lohmann et al., 2004).

of navigation are not immediately apparent (Wiltschko and Wiltschko, 1995).

Chemical cues and navigation

Numerous marine species have well-developed chemical senses that facilitate the detection of food sources over relatively small spatial scales, which often range from centimeters to tens of meters (e.g. Carr, 1988; Weissburg and Dusenbery, 2002; Wyeth et al., 2006). In at least a few cases, however, long-distance migrants have evolved the ability to exploit chemical signals in navigation.

Salmon are the iconic example. Although tremendous variation exists in the life history and migratory patterns of salmon, all hatch in rivers and streams; the young of some species and populations subsequently enter the ocean and disperse across hundreds or thousands of kilometers of open sea (Fig. 5) (Dittman and Quinn, 1996; Quinn, 2005). Several years later, as adults, the fish use

chemical cues to help locate their natal rivers once they have arrived in the general vicinity of the river mouth; such cues also help guide salmon up the correct branches of rivers as they migrate to their spawning grounds (Johnsen, 1982; Johnsen and Hasler, 1980; Døving et al., 1985; Dittman and Quinn, 1996). That the salmon actually 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 development and subsequently released to undergo their normal migrations. These artificially imprinted salmon returned to breed in streams that had been scented with the imprinting chemical (e.g. Hasler and Scholtz, 1983; Dittman et al., 1996; Nevitt and Dittman, 1998).

As salmon complete the ocean phase of their migration and draw close to the mouths of their natal rivers, they often enter estuaries, fjords, or other coastal environments where masses of fresh water encounter seawater. In such areas, the water column sometimes

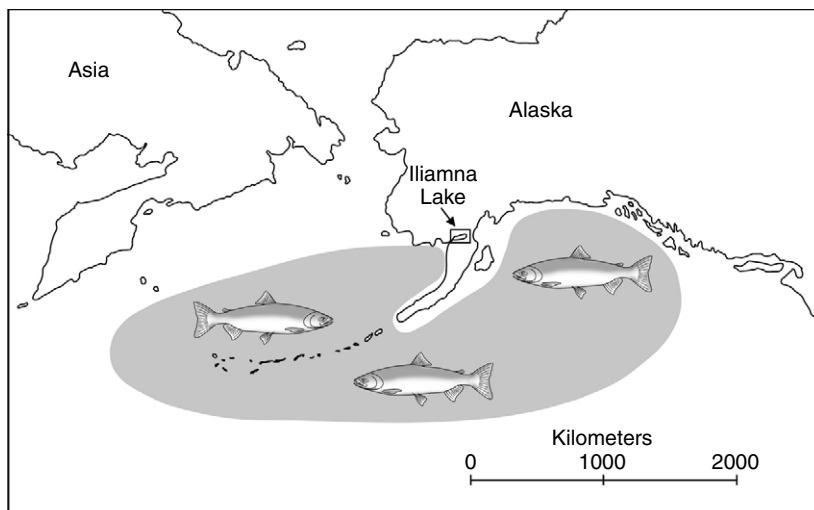


Fig. 5. Ocean distribution of sockeye salmon (*Oncorhynchus nerka*) that spawn in Iliamna Lake, Alaska. Salmon begin their spawning migrations from widely separated locations that are sometimes more than 1000 km from the final target area. Figure modified from Dittman and Quinn (Dittman and Quinn, 1996).

contains multiple layers that remain vertically stratified due to density differences (Døving et al., 1985; Dusenbery, 1992; Moore and Crimaldi, 2004). Salmon move vertically through these layers and, by doing so, may sample differences in chemical cues in the different water masses (Døving et al., 1985). It has been proposed, but not yet demonstrated, that salmon can also detect the relative movements of neighboring layers of water and thus infer the direction in which each water mass is moving (Døving and Stabell, 2003).

Stratified water masses might transport chemical cues from rivers over considerable distances in fjords and other favorable settings where limited vertical mixing occurs. However, such cues cannot persist and extend across more than a thousand kilometers of ocean, the distances over which some populations of salmon are known to migrate (Dittman and Quinn, 1996). For this reason, most authors have concluded that salmon navigation in the open sea is likely to involve a different suite of mechanisms that are not olfactory (e.g. Hasler, 1971; Quinn, 1990; Quinn, 2005; Dittman and Quinn, 1996; Yano et al., 1997; Hinch et al., 2006). The nature of the open-ocean navigation system in salmon, although subject to much speculation, remains unknown.

Hydrodynamic cues: wave direction

Ocean waves are ubiquitous in the open-sea environment and also along exposed continental coastlines. In such coastal areas, wave direction typically provides a reliable indicator of the offshore direction because of wave refraction. As waves approach a coast from the open sea, the leading edge of a wave encounters the ocean bottom first, slowing its forward progress and providing the remainder of the wave crest with an opportunity to catch up. Eventually, the wave approaches the beach directly (i.e. the wave crest is approximately parallel to the shore while moving toward it).

Hatchling sea turtles emerge from underground nests on sandy oceanic beaches, scramble into the sea, and migrate offshore. By swimming into refracted waves, hatchlings launching from the beach can quickly establish courses toward the open sea (Lohmann and Lohmann, 1996a; Lohmann and Lohmann, 2003). Both laboratory (Lohmann et al., 1990; Wyneken et al., 1990) and field experiments (Salmon and Lohmann, 1989; Lohmann et al., 1990; Lohmann and Lohmann, 1992) have demonstrated that hatchlings swim into waves. Additional experiments have demonstrated that hatchlings detect the direction of waves by monitoring the sequence of accelerations that occur within wave orbits below the water's surface (Lohmann et al., 1995b). For example, a turtle facing into oncoming waves is accelerated upward, backward, downward and then forward with each wave cycle, whereas a turtle oriented in the direction of wave movement is accelerated upward, forward, downward and then backward (Fig. 6).

In addition to sea turtles, several invertebrates, including molluscs (Hamilton and Russell, 1982) and arthropods (Nishimoto and Herrnkind, 1978; Rudloe and Herrnkind, 1980), orient to waves or to wave surge. Salmon have been hypothesized to detect and use waves in much the same way that turtles do (Cook, 1984), although experimental confirmation is lacking. An interesting possibility is that marine mammals might also exploit such cues. Seals can detect slight fish-generated water movements (Dehnhardt et al., 2001), so an ability to perceive water movements associated with waves appears plausible.

In some oceanic areas, winds sweep steadily over large expanses of open water and generate waves with long periods and wavelengths, which are known as swells (Bascom, 1980; Bearman,

1989). Because seasonal wind patterns are often relatively constant, the direction of ocean swells is also often seasonally consistent and might, in principle, be used as a directional cue by open-sea migrants (Cook, 1984; Lohmann, 1992). To migrate in different directions, such animals would presumably need to swim at fixed angles relative to waves rather than orienting directly into them as hatchling turtles do. Whether any animal has such a 'wave compass' is not known, but hatchling turtles do have the minimal sensory abilities required, inasmuch as they can distinguish among waves approaching from different angles (Lohmann et al., 1995b). Thus, an interesting speculation is that the tendency of hatchlings to swim directly into waves is supplanted in juvenile and adult turtles by a more versatile ability to use waves as a reference for maintaining any course.

Information in ocean waves might also be used to locate targets in some cases. For example, waves are refracted as they pass around islands, creating characteristic interference patterns on the leeward side (Fig. 7). Traditional Polynesian navigators used such wave patterns to detect the presence of islands too far away to be seen (Lewis, 1978); turtles or other marine animals might do the same. Although no direct evidence for this ability presently exists in animals, a finding of potential interest is that female green turtles captured while nesting on an island and displaced to the leeward side returned more rapidly to the nesting area than turtles displaced an equivalent distance on the windward side (Hays et al., 2003). These results were interpreted initially as evidence that turtles detect windborne odors, but an alternative possibility is that the turtles perceived a change in wave patterns on the downwind (and downwave) side of the island (Fig. 7) (Lohmann et al., 2008).

Hydrodynamic cues: ocean currents

Numerous animals use water currents as a directional cue when crawling short distances or swimming in shallow water. For example, sea slugs (Wyeth et al., 2006), crabs (Weissburg and Dusenbery, 2002) and lobsters (Horner et al., 2004) crawl into water currents in response to chemical cues from prey or potential mates, a response that leads them toward the source of the odor. These animals are thought to monitor current direction by maintaining contact with the substrate, either directly or visually (Dusenbery, 1992). Open-sea migrants, however, lack these stationary reference points and thus are probably unable to use oceanographic currents as directional references. Indeed, analyses of tracks of sea turtles have indicated that, when turtles encounter currents, they do not alter their movements to preserve the original direction of travel; instead currents typically deflect turtles away from their original courses (Girard et al., 2006; Luschi et al., 2007).

Other cues

Although celestial cues are used in orientation and navigation by diverse terrestrial animals (e.g. Wehner et al., 1996; Wiltshko and Wiltshko, 2003; Åkesson and Hedenström, 2007), few studies have investigated these mechanisms in marine species. To our knowledge, no evidence exists for a star compass in any ocean migrant. However, at least a few marine animals are thought to exploit skylight polarization patterns, a sun compass, or both (Quinn, 1980; Quinn, 1982; Avens and Lohmann, 2003). Such cues are presumably available only to animals that swim at or near the air-water interface. The ability of whales to produce sounds that travel long distances, and that might potentially reflect off distant land masses, also provides the basis for interesting speculation, but the logistical obstacles to investigating such a possibility are formidable.

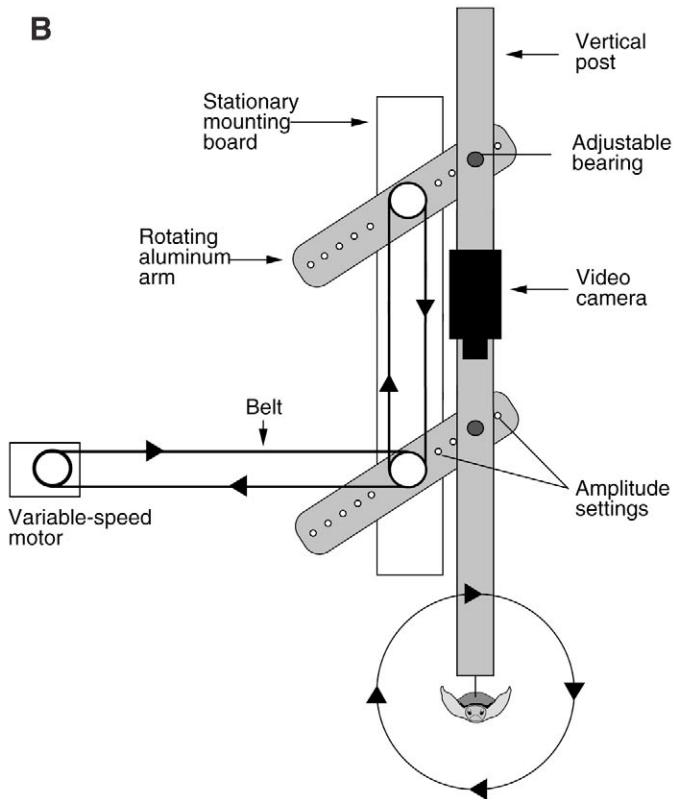
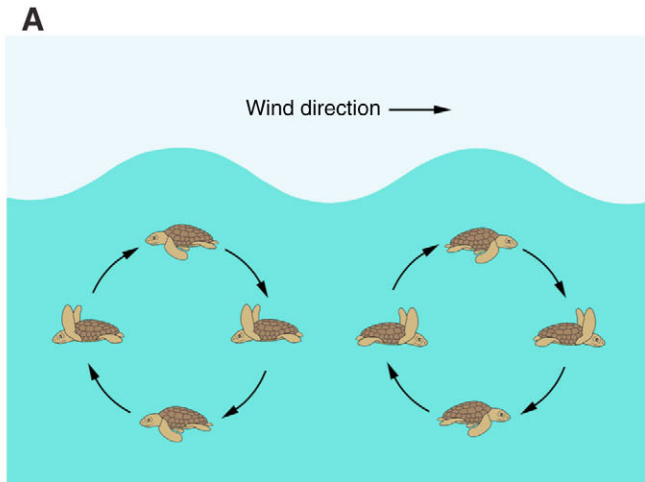


Fig. 6. Perception of ocean wave direction by hatchling sea turtles. (A) The motion of a hatchling turtle swimming with and against the direction of wave propagation. For a hatchling oriented into waves (left), the sequence of accelerations during each wave cycle is upwards, backwards, downwards and forwards. A turtle swimming with the waves (right) is accelerated upwards, forwards, downwards and backwards. Modified from Lohmann and Lohmann (Lohmann and Lohmann, 1992). (B) A machine designed to simulate wave motion by reproducing the sequence of accelerations that occur beneath a propagating wave. The responses of hatchling turtles to these simulated waves have been studied by placing turtles into cloth harnesses (see C) and subjecting them to orbital movements while they are suspended in air. Modified from Lohmann et al. (Lohmann et al., 1995b). (C) A hatchling turtle suspended in air on the wave simulator. Hatchlings suspended in this way act out their normal swimming behavior and will attempt to turn until facing into simulated waves.

Natal homing and biphasic navigation

Despite their phylogenetic differences, sea turtles and salmon have both evolved the ability to exploit disparate, widely separated habitats at different times of their lives. Great diversity exists in the life histories of different populations and species of both groups (Groot and Margolis, 1991; Buskirk and Crowder, 1994; Lutz and Musick, 1997; Quinn, 2005); thus, no general description accurately portrays all members (and indeed, some non-migratory species and populations exist in each case). Nevertheless, some interesting parallels exist among the salmon and sea turtles that undergo the longest oceanic migrations.

The salmon of interest in this context are those that enter the sea from their natal streams and rivers and disperse across hundreds or thousands of kilometers of offshore waters before returning several

years later to their natal tributaries to spawn (Dittman and Quinn, 1996; Quinn, 2005). In the Pacific northwest, this description applies to some populations of sockeye salmon (*Oncorhynchus nerka*), chinook salmon (*O. tshawytscha*) and chum salmon (*O. 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 (Quinn et al., 1999; Quinn, 2005).

Sea turtles of most species migrate intermittently throughout their lives. As hatchlings, turtles migrate offshore; as they grow, many follow complex, population-specific migratory pathways that sometimes lead across entire ocean basins and back (Lutz and Musick, 1997). Older juveniles of some species, such as loggerheads and green turtles, eventually leave the open-ocean environment and take up residence in neritic feeding grounds, sometimes migrating

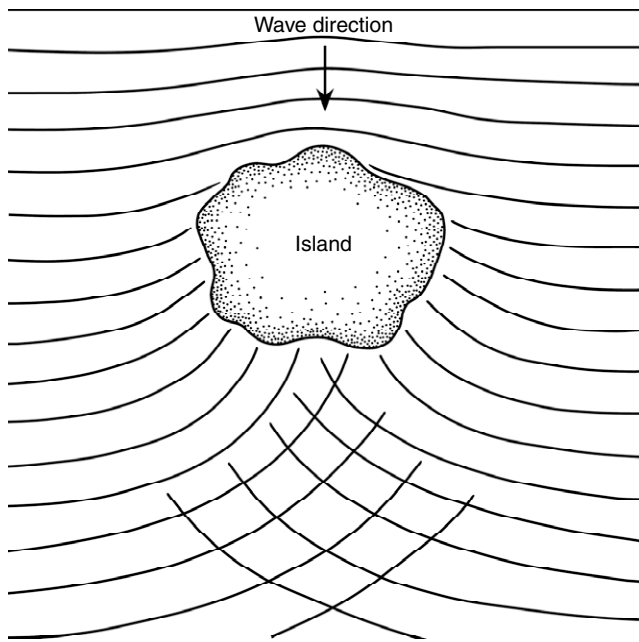


Fig. 7. Diagram of wave refraction patterns around an island in the open ocean. As waves pass around an island, the parts that encounter shallow water are slowed relative to the parts remaining over deeper water. As a result, refraction occurs and a pattern of wave interference often forms on the leeward side of the island.

seasonally between summer and winter habitats. As adults, turtles of nearly all species migrate intermittently from their feeding grounds to specific mating and nesting areas and back again. Genetic analyses have confirmed that the adults of many (and perhaps most) populations return to their natal region for nesting (Meylan et al., 1990; Bowen et al., 1993; Bowen et al., 1994; Bowen et al., 1995). Although some populations demonstrate exceedingly precise natal homing, others may only home to regions of coastline several hundred kilometers in length (Bjørndal et al., 1983; Peare and Parker, 1996; Lee et al., 2007); at a minimum, natal homing is regional in nature (Bowen and Avise, 1995; Miller, 1997).

Although sea turtles and salmon have been investigated independently and through somewhat different means, an interesting similarity has emerged: both have been hypothesized to complete long-distance reproductive migrations using navigational systems composed of two different suites of mechanisms that function sequentially over different spatial scales (Quinn, 2005; Lohmann et al., 2008). In each case, the first navigational system is thought to guide the animals across large expanses of ocean and bring them into the general vicinity of the target area. The second system is then thought to supplement the first and lead animals to their final destination (the correct branch of a river for salmon and a nesting area for sea turtles).

If this view is correct, then what is the basis of the dual navigational systems in each of these groups of animals? In turtles, direct experimental evidence for a magnetic map sense has been acquired (Fig. 4) (Lohmann et al., 2004) and this mechanism might plausibly guide turtles over hundreds or thousands of kilometers into the general vicinity of a nesting beach (Lohmann et al., 1999; Luschi et al., 2007). However, the existence of magnetic anomalies, and the fact that the Earth's field changes gradually over time, are likely to make the resolution of such a map too imprecise to guide turtles to highly specific nesting areas (Lohmann et al., 1999;

Lohmann et al., 2008). Thus, the involvement of additional local cues must be hypothesized once a turtle reaches the vicinity of its target (e.g. Lohmann et al., 1999; Hays et al., 2003; Lohmann et al., 2008).

The situation with salmon differs from that of sea turtles in that it is the second navigation system that is well characterized and the first that is enigmatic. Much is known about how salmon use chemical cues to pinpoint their natal rivers once they are near, but how they navigate into the correct vicinity from hundreds of kilometers away remains a matter of speculation. Techniques developed for studying navigation in sea turtles under laboratory conditions (e.g. Lohmann et al., 2001; Lohmann et al., 2004) might provide a possible approach for gaining insight into how salmon guide themselves in the open sea.

Given our present understanding, it seems possible that the navigational systems of sea turtles and salmon are more alike than different. Salmon might rely on a magnetic map like that of turtles to navigate into the vicinity of their natal rivers, close enough for chemical cues to be detected; sea turtles might use olfactory cues in the final stages of returning to their natal beaches. Both animals might use hydrodynamic cues (waves) as an orientation cue under appropriate conditions. If so, the basic navigational processes in these two seemingly different long-distance migrants might be very similar, and perhaps representative of other long-distance ocean navigators as well. Many additional studies will be needed to determine whether different migrants do indeed use similar navigational mechanisms and strategies, or whether each has evolved a different method of finding its way in the sea.

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