12

THE GEOMAGNETIC SENSE OF CRUSTACEANS AND ITS USE IN ORIENTATION AND NAVIGATION

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Abstract

Most crustaceans are active, mobile organisms that periodically move through complex environments in search of food, shelter, and mates. In many cases, movements are not random, but instead are directed toward specific targets. On a small spatial scale, destinations can be burrows or other refuges, such as wetter or drier microhabitats; on a larger scale, targets can include locations suitable for larval release or offshore habitats for overwintering. Efficient movement between ecologically important locations has presumably been favored by natural selection, and crustaceans have evolved a suite of guidance mechanisms suitable for directing the movements they make. Among the numerous sensory cues potentially available to terrestrial and aquatic crustaceans, the Earth's magnetic field is a particularly pervasive cue that is continuously available in nearly all environments that crustaceans inhabit. At least some crustaceans have evolved the ability to perceive the Earth's field. Various amphipods, isopods, and spiny lobsters possess magnetic compasses, which enable them to maintain headings toward particular directions such as north or south. In principle, the Earth's field also provides a potential source of positional or "map" information that can help an animal navigate toward a specific target area. The Caribbean spiny lobster, Panulirus argus, has been shown to possess such a magnetic map, which allows lobsters to determine their geographic location relative to a goal. Although behavioral studies have demonstrated that some crustaceans perceive the Earth's magnetic field, little is known about how they do so. At present, three main mechanisms of magnetoreception have been proposed: electromagnetic induction, magnetite, and chemical magnetoreception. Further studies are needed to determine how widespread magnetoreception is among crustaceans and to investigate the physical basis of the magnetic sense.

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INTRODUCTION

The remarkable diversity of crustacean lifestyles is accompanied by extreme variation in movement patterns. A few species are sedentary, epitomized by barnacles that spend their entire adult lives irreversibly anchored to a hard substratum in a single location. Most crustaceans are mobile to varying degrees, but patterns of movement, as well as the spatial scales traveled, vary greatly among different groups and species. For example, some crustaceans migrate up and down the beach with the tides (Cubit 1969, Forward et al. 2005, Scapini 2006). Others, such as semiterrestrial crabs, forage over relatively small distances from a burrow but retreat to it when approached by predators (Hughes 1966, Vannini and Cannicci 1995, Zeil 1998). Still others undergo long-distance migrations of considerable duration and complexity (Herrnkind and Kanciruk 1978, Adamczewska and Morris 1998, Tankersley et al. 1998). In all of these cases, survival is enhanced by an ability to orient movements reliably and efficiently toward destinations, regardless of whether the goal is a moist patch of sand, a burrow, or a distant area used for overwintering or larval release.

Mobile marine animals exploit numerous types of sensory information while migrating, homing, or moving around their habitats (Lohmann et al. 2008). Among these, the Earth's magnetic field is unusually reliable and pervasive. In contrast with most other sensory cues, the field is present both night and day, is largely unaffected by weather and season, and exists virtually everywhere in the marine environment, from salt marshes and maritime forests to the deepest ocean trenches. Thus, it is perhaps not surprising that some crustaceans have evolved ways to exploit the geomagnetic field to guide their movements. In this chapter, we review what is known about how crustaceans perceive the Earth's field and use it in orientation and navigation.

THE EARTH'S MAGNETIC FIELD

To a first approximation, the Earth's magnetic field resembles the dipole field of a giant bar magnet (Fig. 12.1). Field lines leave the southern hemisphere and curve around the globe before reentering the planet in the northern hemisphere.

Animals can potentially extract at least two different kinds of information from the Earth's field. The simplest is directional information, which enables an animal to maintain a consistent heading (e.g., toward the north or south). Animals with this ability are said to have a magnetic compass. Some animals also derive positional information from the Earth's field; in other words, they can use magnetic cues to assess where they are located relative to a goal, or to determine what direction to travel at a particular location along a complex migratory route (Lohmann et al. 2007, 2012). Animals that derive positional information from the field are said to have a magnetic map. This term is used as convenient shorthand and does not imply that the map is necessarily detailed or organized in the same way as a human map (Lohmann 2010).

We will begin by looking at how crustaceans use directional information in the Earth's magnetic field. Magnetic compasses have been shown to exist in amphipods, isopods, and spiny lobsters.

A MAGNETIC COMPASS IN AMPHIPODS AND ISOPODS

Amphipods, also known as sandhoppers or beachhoppers, are common inhabitants of intertidal zones. Many species move with the tides to remain in damp sand, following the receding water to avoid desiccation as the tide falls, but retreating before the rising tide to avoid inundation

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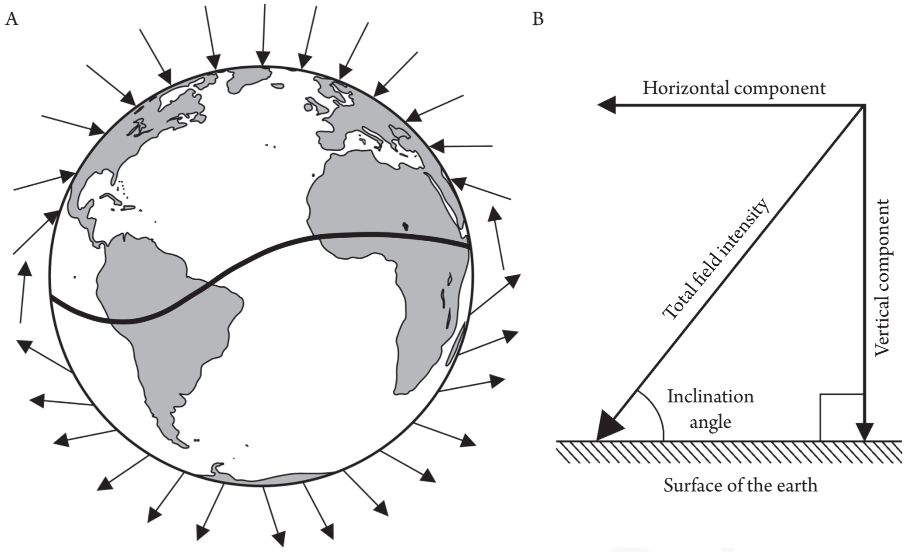

Fig. 12.1.
(A) Diagram of the Earth's magnetic field, illustrating how field lines (represented by arrows) intersect the Earth's surface, and how inclination angle (the angle formed between the field lines and the Earth) varies with latitude. At the magnetic equator (the curving line across the Earth), 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 degrees. (B) Diagram illustrating four elements of geomagnetic field vectors that might, in principle, provide animals 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. Diagram is from Lohmann et al. 2007, with permission from The Company of Biologists.

(Scapini 2006). This type of orientation, in which an animal moves mainly along an axis perpendicular to a waterline, is often referred to as Y-axis orientation (Wiltschko and Wiltschko 1995a). The orientation cues that underlie Y-axis orientation in amphipods have been studied extensively and include several different kinds of environmental information, including visual landscape cues, sun compass orientation, and beach slope (e.g., Pardi and Scapini 1983, Pardi and Ercolini 1986, Ugolini et al. 1988).

Early attempts to demonstrate magnetic orientation in amphipods produced contradictory results. Experiments carried out in coastal areas of several European countries indicated that the amphipod *Talitrus saltator*, when tested in complete darkness, was able to orient nonrandomly (Van den Bercken et al. 1967). The Earth's magnetic field was considered as a possible orientation cue, but an initial attempt to disrupt the orientation by canceling the ambient field was unsuccessful. In a subsequent study conducted in Italy, Ercolini and Scapini (1972) were unable to replicate the finding of nonrandom orientation in darkness. Working in The Netherlands, however, Arendse (1978, 1980, Arendse and Kruyswijk 1981) reported orientation of *Talitrus* in directions coinciding with the land-sea axis. When the ambient field was rotated to a new position, the orientation shifted accordingly; when the ambient field was eliminated, the orientation vanished. These results provided the first clear evidence for magnetic sensitivity in a crustacean.

Arendse and Kruyswijk (1981) also reported that amphipods in the process of jumping aligned themselves with the field, whereas crawling amphipods did not. This provided a possible

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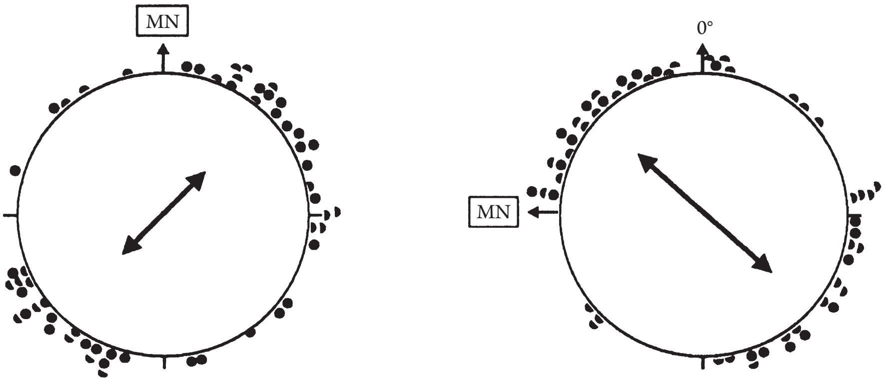

Fig. 12.2.
Orientation of the marine isopod *Idotea baltica basteri* tested in an arena under two different magnetic fields. (A) Isopods tested in a natural magnetic field oriented along a magnetic axis that coincided with the seaward-landward axis in their natural environment. (B) Isopods tested in an artificial magnetic field in which magnetic north (MN) was rotated counterclockwise by 90 degrees showed a corresponding shift in orientation. Each circle or half circle on the diagram reflects the orientation of one isopod. Full circles indicate the direction of individuals that had unimodal orientation (i.e., moved consistently in one direction). Half circles indicate individuals with bimodal orientation (i.e., they moved in one direction in approximately half of the trials and the opposite direction in the other half). The double-headed arrows in the center of each circle indicate the axis along which each group of isopods moved. Diagram is modified from Ugolini and Pezzani (1995), with permission from Elsevier.

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explanation for why earlier studies, which did not distinguish between crawling and jumping animals, might have failed to provide evidence for magnetic orientation. A subsequent study in Italy, however, again failed to find evidence for magnetic orientation (Scapini and Quochi 1992). It is possible that the different outcomes reflect population differences between amphipods in Italy and The Netherlands, or perhaps a difference in the importance of various local cues present at the specific beaches where the different studies were done (Wiltschko and Wiltschko 1995a). In an additional study carried out in Italy, Ugolini (1994) reported that altering the ambient field affected the orientation of *Talitrus*, but the quadrimodal orientation he observed differed from the bimodal orientation observed previously in The Netherlands.

Similar experiments with the African amphipod *Talorchestia martensii* demonstrated that individuals oriented along the Y-axis of their home beach in complete darkness under the natural magnetic field, but oriented randomly when the magnetic field was canceled (Ugolini and Pardi 1992). Subsequent experiments designed to investigate interactions between the magnetic compass and the sun compass revealed that, when amphipods were tested with a view of the sun but in a magnetic field rotated 90 degrees clockwise, orientation was quadrimodal. Approximately half of the animals oriented along an axis coinciding with the real land-sea axis, whereas the other half oriented along the magnetic axis that had formerly coincided with the land-sea axis. These results are consistent with the hypothesis that the magnetic compass and sun compass are both used in Y-axis orientation, and that different individuals preferentially weigh one or the other if the cues are placed in conflict, a situation that never arises in nature. Additional experiments have shown that, when solar cues are absent, these amphipods use the geomagnetic field as the primary orientation cue (Ugolini et al. 1999, Ugolini 2001, 2002).

Ugolini and Pezzani (1995) reported similar findings in the marine isopod *Idotea baltica*. Like the amphipods, *Idotea* oriented along the land-sea axis when tested in the natural magnetic field. When the ambient field was rotated to a new position, orientation shifted accordingly (Fig. 12.2). When the horizontal component of the field was canceled, orientation became random.

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The isopods were also able to learn to orient in magnetic directions corresponding to directions that take them up or down slope, a response that would presumably help guide Y-axis orientation under natural conditions. Isopods exposed to a slope aligned perpendicular to the actual land-sea axis quickly learned to move along the magnetic axis corresponding to the new up-down slope direction, a directional preference expressed even when testing was done on a horizontal surface. These results imply that isopods can determine the land-sea axis in their environment using slope, and can then use a magnetic compass to move in appropriate directions during Y-axis orientation.

A MAGNETIC COMPASS IN SPINY LOBSTERS

A magnetic compass sense has also been discovered in the Caribbean spiny lobster *P. argus*. In some geographic areas, this species undergoes an annual mass migration in which thousands of lobsters vacate shallow, inshore areas and crawl seaward in single-file, head-to-tail processions (reviewed by Kanciruk and Herrnkind 1978, Herrnkind 1980). Lines of spiny lobsters within the same geographical area follow nearly identical compass bearings (Herrnkind et al. 1973).

Field and laboratory experiments have demonstrated that spiny lobsters can detect wave surge (the horizontal movement of water near the ocean floor) and use it as a directional cue (Walton and Herrnkind 1977, Nevitt et al. 1995). Migratory orientation persists, however, in areas where hydrodynamic cues are disrupted or absent, and when visual cues are obscured by turbid water or darkness (Herrnkind 1970, Herrnkind and McLean 1971).

In an initial attempt to determine whether spiny lobsters orient magnetically, Walton and Herrnkind (1977) captured lobsters in nonmigratory condition, covered their eyes, and displaced them to a new location. The orientation of ten lobsters carrying magnets was compared to the orientation of the same individuals carrying nonmagnetic solder wire as a control. Under these conditions, lobsters oriented into the prevailing wave surge regardless of whether magnets were attached. Although the results provided no evidence that spiny lobsters orient magnetically, the possibility that they use magnetic cues under different circumstances (e.g., in the absence of wave surge) could not be ruled out.

In a subsequent laboratory experiment, an attempt was made to condition spiny lobsters to orient toward specific magnetic directions to receive food rewards (Lohmann 1985). Several lobsters were trained and tested in a rotatable circular orientation apparatus in which they could enter tunnels aligned with different compass directions. Two lobsters that had received positive reinforcement for orienting along a north-south magnetic axis were tested in the Earth's field and in a field in which magnetic north was rotated 60 degrees clockwise. In each case, lobsters entered the tunnels aligned with magnetic north-south more often than expected by chance, providing initial evidence for magnetic sensitivity.

Direct evidence for a magnetic compass in spiny lobsters was subsequently obtained in experiments carried out inside an underwater magnetic coil system located on a patch reef in the Florida Keys (Lohmann et al. 1995; Fig. 12.3). Lobsters were captured on the reef, and their eyestalks were covered with rubber eye caps to eliminate visual cues. Each animal was then tethered on a flat Plexiglas surface inside the coil. As the lobster walked, it was held in place by the tether, but its feet slipped across the surface. Most lobsters tethered in this way established and maintained consistent headings toward specific directions.

After a lobster had established a consistent heading, it was exposed to either a reversal of the horizontal component of the Earth's field, or to no change in the ambient field (controls). Those animals subjected to the field reversal deviated significantly from their initial courses, whereas

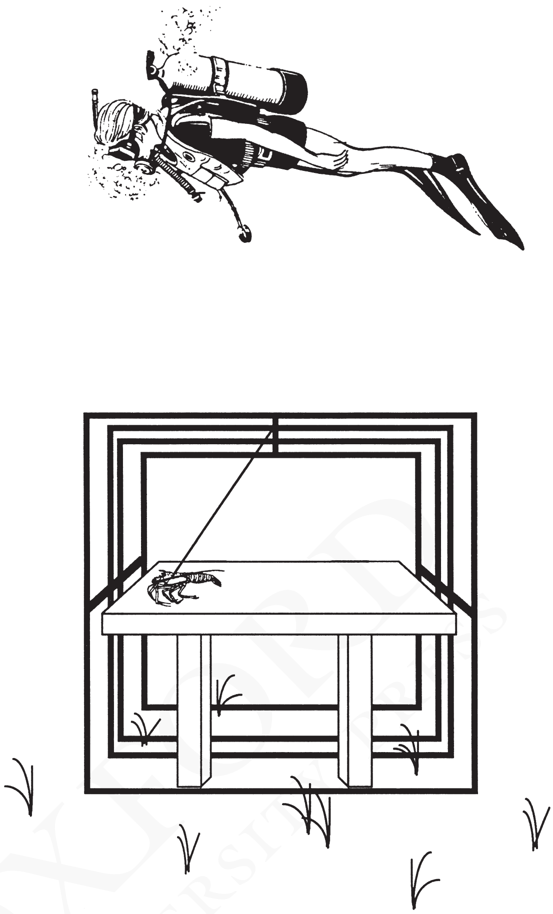

Fig. 12.3.
Underwater magnetic coil system and tethering procedure used to demonstrate the existence of a magnetic compass in spiny lobsters (from Lohmann et al. 1995, with permission from The Company of Biologists). See text for details.

control lobsters did not (Fig. 12.4). These results demonstrated that spiny lobsters have a magnetic compass sense and can use it to maintain headings in their natural habitat.

Two functionally different types of magnetic compasses have been reported in animals. Polarity compasses, which are present in salmon (Quinn et al. 1981) and mole rats (Marhold et al. 1997), determine north using the polarity of the horizontal field component. By contrast, the inclination compasses of birds (Wiltschko and Wiltschko 1972) and sea turtles (Light et al. 1993, Goff et al. 1998) evidently do not detect the polarity of the field (i.e., north vs. south). Instead, they define "poleward" as the direction along the Earth's surface in which the angle formed between the magnetic field vector and the gravity vector is smallest. Some salamanders have both types of compasses and use each in different behavioral tasks (Phillips 1986).

To determine whether spiny lobsters have a polarity or inclination compass, Lohmann et al. (1995) exposed one group of lobsters tested in the underwater coil to a field with the vertical component of the field inverted, a treatment that does not affect animals with a polarity compass but that elicits a reversal of orientation direction in animals with an inclination compass.

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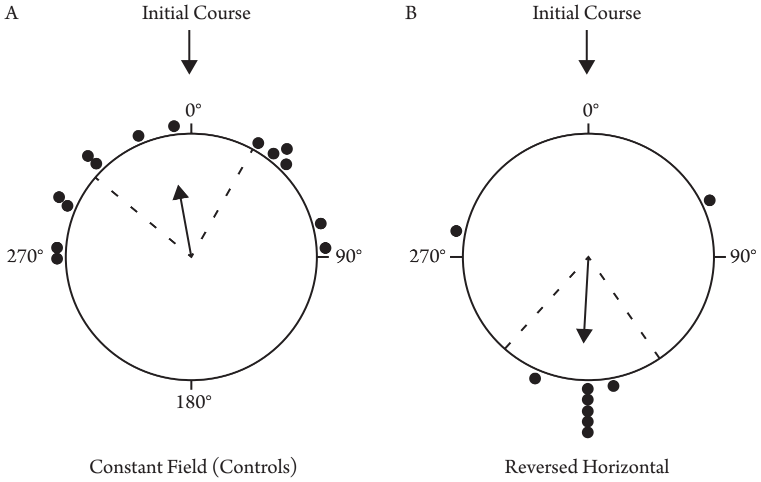

Constant Field (Controls)

Reversed Horizontal

Fig. 12.4.
Maximum deviations of spiny lobsters from initial paths established in the Earth's magnetic field. The direction that each lobster walked initially was normalized to 0 degrees. (A) In trials in which the field was not changed, lobsters seldom deviated from the initial heading by more than 90 degrees. (B) In trials in which the horizontal field direction was reversed, lobsters had an average maximum deviation of 180 degrees. The arrows in the center of each circle indicate significant mean angles; the length of the arrow is proportional to the mean vector length r, with r = 1 represented by the edge of the circle. Dotted lines represent 95% confidence intervals for the mean angles. Diagram is modified from Lohmann et al. 1995, with permission from The Company of Biologists.

The orientation of the lobsters did not change, implying that they have a polarity compass functionally similar to that of salmon and mole rats.

Although spiny lobsters have a magnetic compass, whether it is used to guide the autumn migration is not known. The hypothesis appears plausible but has not yet been tested experimentally, inasmuch as all studies on magnetic orientation have been carried out with lobsters that are not in migratory condition.

HOMING IN SPINY LOBSTERS

The Caribbean spiny lobster is capable of at least some navigational tasks that cannot be explained by a magnetic compass alone. Working in Bermuda, Creaser and Travis (1950) captured and marked a number of spiny lobsters before displacing them to various locations. A surprising number (about 20%) were recaptured after displacement, including some that were released in deep water (1500 m) and had to travel in excess of 8 km to return to the capture sites. These findings led Creaser and Travis (1950) to conclude that these lobsters possess "a remarkable homing instinct," the basis of which was unknown at the time.

Subsequent studies revealed that the ability to return reliably to a home area appears to be a natural component of the behavior of this species. Juvenile and adult spiny lobsters spend daylight hours hidden inside coral reef crevices or holes, emerging at night to forage over a considerable area before returning in darkness to the same den or to one of several others nearby (Herrnkind et al. 1975, Herrnkind and Redig 1975).

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TRUE NAVIGATION IN SPINY LOBSTERS

In the animal navigation literature, an animal is said to be capable of true navigation if, after displacement to a location where it has never been, it can determine its position relative to a goal without relying on familiar surroundings, cues that emanate from the destination, or information collected during the outward journey. In an experiment designed to determine whether spiny lobsters are capable of true navigation, lobsters in the Florida Keys, United States, were captured and transported by indirect, circuitous routes to test sites 12–37 km away from the capture site (Boles and Lohmann 2003). The animals were transported inside closed, opaque plastic containers partly filled with sea water, preventing access to visual cues and ensuring that they could not access chemical cues along the way. In some experiments, lobsters were also subjected to strong, varying magnetic fields during transport, to ensure that they could not use their magnetic compass to monitor the outward trip.

At the test site, lobsters were permitted to sit overnight in the undisturbed magnetic field of the Earth before their orientation was tested the following morning. During tests, the lobsters were tethered so that they could walk in place inside a water-filled orientation arena. To ensure that the lobsters had never visited the test sites previously, the arena was placed on land. To prevent access to visual cues, the eyestalks of each animal were covered with rubber eye caps (Lohmann et al. 1995).

Remarkably, lobsters tested in this way oriented in directions that, on average, coincided with paths back toward the site of capture (Fig. 12.5). These findings are consistent with the earlier homing studies of Creaser and Travis (1950) and imply that spiny lobsters are somehow able to determine their position relative to the capture site. Moreover, given that the animals were deprived of all known sources of positional information during transport, spiny lobsters appear to assess their geographic location based on information present at the test site (Boles and Lohmann 2003).

MAGNETIC MAPS IN SPINY LOBSTERS

How spiny lobsters determine their position after being displaced to locations where they have never been was not immediately apparent. However, several features of the Earth's field vary across the globe in such a way that they might, in principle, be used in position finding (Fig. 12.1). For example, at each geographic location, 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 Earth's surface, 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 if it is north or south of a particular area. Sea turtles are known to be capable of this (Lohmann and Lohmann 1994).

In addition to inclination angle, at least three other magnetic field elements vary across the Earth's surface in ways that make them suitable for a position-finding sense (Skiles 1985, Lohmann et al. 1999, Putman et al. 2011). These include: (1) the intensity (strength) of the total field; (2) the intensity of the horizontal field; and (3) the intensity of the vertical field.

To determine whether spiny lobsters possess "magnetic maps" that can be used to assess their position relative to their home areas, lobsters captured in the middle Florida Keys were placed into a circular pool of water so that their orientation could be monitored as described

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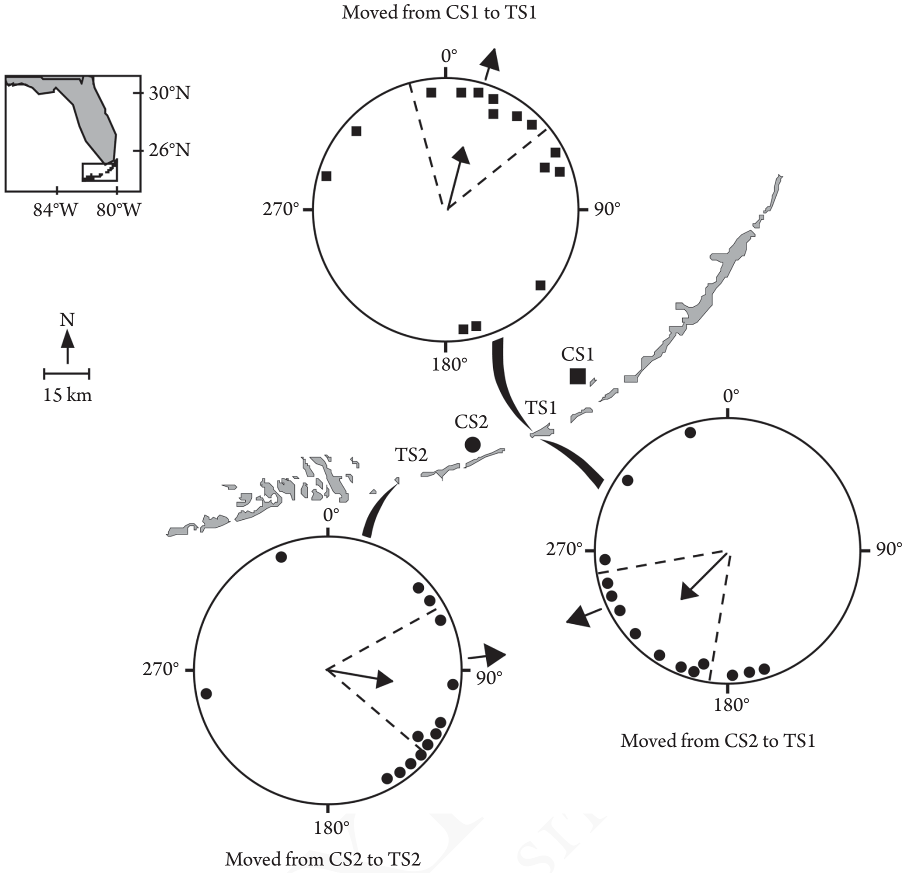

Fig. 12.5.
Homing in displaced spiny lobsters. Spiny lobsters were transported by boat from two capture sites (CS1, CS2) via circuitous routes to one of two test sites (TS1, TS2). In the orientation diagrams, each small symbol represents the mean angle of a single spiny lobster. Squares indicate spiny lobsters captured at CS1, whereas circles indicate spiny lobsters captured at CS2. The arrow in the center of each orientation diagram indicates the mean angle of each group and the dotted lines represent the 95% confidence interval for the mean. The arrow outside each orientation diagram indicates the direction from the test site to the capture site. In each case, the mean angle of orientation coincided closely with the direction toward the capture site. Modified from Boles and Lohmann (2003), with permission from the Nature Publishing Group.

previously. This time, however, a large magnetic coil system was constructed around the pool so that lobsters could be tested in specific fields replicating those that exist in particular geographic areas (Boles and Lohmann 2003).

Lobsters tested in a field that exists north of the capture site oriented southward, whereas those tested in a field like one that exists south of the capture site oriented northward (Fig. 12.6). These findings indicate that lobsters exploit magnetic information as a component of a classical navigational map which facilitates navigation to specific geographic locations. A lobster's ability to navigate back to its home area appears to be based at least partly on the animal's experience and learned understanding of how the Earth's field varies in the geographic region where it lives (Lohmann and Lohmann 2006).

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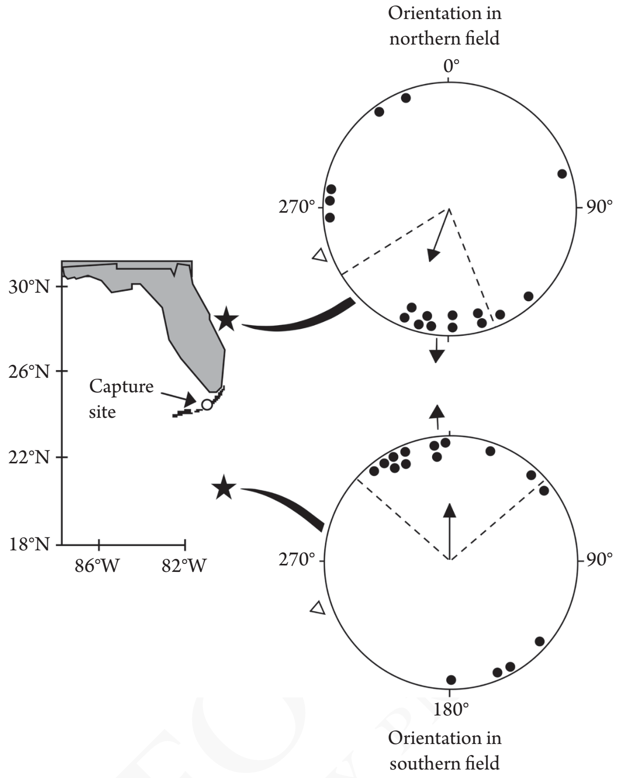

Fig. 12.6.
Evidence for a magnetic map in spiny lobsters. The diagram shows orientation of spiny lobsters tested in magnetic fields replicating those that exist at two different geographic locations (marked by stars on the map). Spiny lobsters were captured at Grassy Key (CS2 on Fig. 12.5), transported to the testing site (TS1 on Fig. 12.1), and held overnight in the local magnetic field before being tested in the morning. Spiny lobsters tested in a field like one that exists north of the test site walked southward, whereas those tested in a field like one that exists south of the test site walked northward. The open triangle outside each orientation diagram indicates the actual direction to the capture site from the test site. In each case, spiny lobsters responded as if they had been displaced to the locations marked by the stars rather than by orienting in the direction that was actually toward the capture site. Modified from Boles and Lohmann (2003), with permission from the Nature Publishing Group.

MECHANISM OF MAGNETIC FIELD DETECTION

The mechanism or mechanisms underlying magnetic field detection have not been clearly established in any crustacean. Indeed, a full understanding of how any animal perceives magnetic fields has not yet been attained (Wiltschko and Wiltschko 2005, Johnsen and Lohmann 2005, 2008, Lohmann 2010). In recent years, most discussion of possible mechanisms underlying magnetoreception has focused on three main ideas: electromagnetic induction, magnetite, and chemical magnetoreception. We will consider these in turn, with special reference to the relevance of each to crustaceans.

Electromagnetic Induction

When an object composed of an electrically conductive material moves through a magnetic field in any direction other than parallel to the field lines, positively and negatively charged particles

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migrate to opposite sides of the object, resulting in a constant voltage that depends on the speed and direction of the object's motion relative to the magnetic field (Purcell 1985, Johnsen and Lohmann 2005, 2008). If the object is immersed in sea water (or any other conductive medium) that is stationary relative to the field, an electric circuit is formed and current flows through the medium and object.

This principle of electromagnetic induction might explain how elasmobranch fish (sharks, skates, and rays) perceive magnetism (Kalmijn 1974, 1984). Because the bodies of these animals are conductive and the fish have highly sensitive electroreceptors, elasmobranchs might detect the voltage drop of the induced current that arises as they swim through Earth's field (Lohmann and Johnsen 2000, Johnsen and Lohmann 2008). However, whether these fish actually perceive magnetic fields in this way is not known.

In contrast to the situation in elasmobranchs, structures that serve as electroreceptors have never been identified in crustaceans. Recent reports, however, have provided behavioral evidence that crayfish may nevertheless perceive weak electric fields, an ability hypothesized to function in helping the animals detect hidden prey (Patullo and Macmillan 2007, 2010). If electroreceptors are confirmed to exist in crustaceans, then a magnetoreception mechanism based on electromagnetic induction is hypothetically possible. At present, however, the reported level of sensitivity to electrical stimuli by crayfish appears insufficient for crustaceans to exploit this mechanism in sensing the Earth's magnetic field (Patullo and Macmillan 2010), or perhaps even in sensing prey (Steullet et al. 2007).

Magnetite

Some bacteria and unicellular algae orient their movements along magnetic field lines (Bazylinski and Frankel 2004). The discovery that crystals of the magnetic minerals magnetite (Fe_3O_4) and greigite (Fe_3S_4) underlie this ability has inspired searches for similar minerals in diverse animals. Magnetite was subsequently detected in birds, salmon, sea turtles, and a number of other animals that are known to orient to the Earth's magnetic field (Kirschvink et al. 1985).

Most magnetite isolated from animals has been in the form of single-domain magnetite crystals similar to those found in magnetotactic bacteria (Johnsen and Lohmann 2005, 2008). Single-domain magnetite crystals are minute (about 50 nm in diameter), permanently magnetized magnets that twist into alignment with the Earth's magnetic field if allowed to rotate freely.

In principle, such crystals might transduce geomagnetic field information to the nervous system in several different ways. One possibility is that magnetite crystals exert torque or pressure on secondary receptors (such as stretch receptors, hair cells, or mechanoreceptors) as the particles attempt to align with the geomagnetic field. Alternatively, the rotation of intracellular magnetite crystals might open ion channels directly if, for example, cytoskeletal filaments connect the crystals to the channels. Additional ways that magnetite might interact with the nervous system have also been proposed (see Kirschvink et al. 2001, Johnsen and Lohmann 2005, Walker 2008 for more examples).

Magnetic material that might be involved in magnetoreception has been detected in the Caribbean spiny lobster *P. argus* (Lohmann 1984). The material is concentrated primarily in the cephalothorax, especially in tissue associated with the fused thoracic ganglia. Although direct evidence that magnetite underlies magnetoreception in spiny lobsters has not been obtained, findings consistent with this hypothesis have been acquired through pulse magnetization experiments (Cain 2001). A strong magnetic field of brief duration can be used to alter the direction of magnetization in magnetite particles. Pulse magnetization might, therefore, alter magnetite-based magnetoreceptors and change the behavior of animals that use such receptors

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to derive directional or positional information from the Earth's field. In studies with several animals, including spiny lobsters (Cain 2001), the application of strong magnetic pulses either randomized the preferred orientation direction or else deflected it relative to controls (Wiltschko and Wiltschko 1995b, Beason et al. 1997, Irwin and Lohmann 2005). These results have generally been interpreted as evidence for magnetite-based magnetoreceptors, although other explanations cannot be ruled out with certainty (Johnsen and Lohmann 2005). In principle, strong magnetic pulses might alter magnetite-based receptors that are part of a compass sense, a map sense, or both. Additional research will be needed to determine whether magnetoreception in spiny lobsters is mediated by magnetite-based receptors.

Chemical Magnetoreception

A third hypothesis proposes that magnetoreception involves unusual biochemical reactions that are influenced by the Earth's magnetic field. Because these reactions involve pairs of free radicals as fleeting intermediates, this idea is also known as the radical pairs hypothesis.

The details of this proposed mechanism are complex and have been described elsewhere (Johnsen and Lohmann 2008, Rodgers and Hore 2009, Ritz et al. 2010). If chemical magnetoreception occurs, then it may be associated with the visual system (Liedvogel and Mouritsen 2010, Ritz et al. 2010). Many of the best-known radical-pair reactions begin with electron transfers that are induced by the absorption of light (Johnsen and Lohmann 2008, Ritz et al. 2010). This has led to the suggestion that chemical magnetoreceptors might also be photoreceptors. The possible link to photoexcitation has also led to interest in blue-light-sensitive photoreceptive proteins known as cryptochromes (Liedvogel and Mouritsen 2010). Cryptochromes are attractive candidates for magnetoreceptors because they exist in diverse animals and have a chromophore that forms radical pairs after photoexcitation (Johnsen and Lohmann 2005). Some evidence consistent with the hypothesis that cryptochromes function in magnetoreception has been obtained in migratory birds (Rodgers and Hore 2009, Ritz et al. 2010). The strongest evidence for cryptochrome involvement, however, comes from experiments with the fruit fly *Drosophila*, in which flies were trained to enter one arm of a simple maze on the basis of magnetic-field conditions. Mutant flies lacking genes for cryptochrome were unable to perform this task, but magnetic sensitivity was restored when cryptochrome genes were inserted into the flies (Gegear et al. 2008).

If animals perceive magnetic fields using chemical reactions that occur within the visual system, then it is possible that they see, superimposed on their visual field, an additional signal consisting of a pattern of lights or colors, which changes depending on the magnetic direction that the animal faces (Lohmann 2010). Some indirect evidence exists to support this idea. For example, birds failed to orient magnetically when the right eye (which is known to be dominant in tasks involving object perception) was covered with a frosted foil that blurred vision, a result consistent with the hypothesis that interactions exist between processing visual patterns and detecting magnetic directions (Stapput et al. 2010). In crustaceans, however, no studies have been carried out investigating the possibility of chemical magnetoreception.

FUTURE DIRECTIONS

The study of magnetoreception in crustaceans is still in its infancy. At present, studies have been conducted with only a few species, but the existence of magnetic sensitivity in several

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different groups (amphipods, isopods, and lobsters) suggests that the ability to perceive magnetic fields might be widespread among crustaceans, and perhaps among arthropods more generally (e.g., Arendse 1978, Baker 1987, Phillips and Sayeed 1993, Gegear et al. 2008). Investigations with diverse crustaceans appear likely to expand the list of species known to perceive magnetic fields.

The Caribbean spiny lobster *P. argus* is the most thoroughly studied crustacean in terms of magnetoreception, yet numerous questions remain about exactly how this species exploits geomagnetic information. For example, although the lobsters' "magnetic map" is thought to rely on magnetic field parameters such as intensity and field inclination (Boles and Lohmann 2003), the precise way in which the map is organized is not understood (Lohmann and Lohmann 2006, Lohmann et al. 2007). Similarly, the capabilities and limitations of the map have not yet been investigated, nor is it known how the magnetic compass and map function during the seasonal migrations of these lobsters.

Finally, almost nothing is known about the neural mechanisms that underlie magnetic field detection in crustaceans. Although the existence of magnetic material in spiny lobsters (Lohmann 1984) is consistent with the hypothesis that magnetite serves as the physical basis for the magnetic sense, definitive evidence for magnetite-based magnetoreception is lacking. Clearly, research on a number of different fronts appears likely to result in major advances.

SUMMARY AND CONCLUSIONS

Representatives of several crustacean groups, including amphipods, isopods, and spiny lobsters, have magnetic compasses that enable them to orient movements relative to the Earth's magnetic field. In addition, the Caribbean spiny lobster has a magnetic map sense, which allows it to use positional information in the Earth's field to navigate toward its home area. Little is known about the mechanism(s) that underlie magnetic field detection in crustaceans. Evidence consistent with magnetite-based receptors has been obtained in the spiny lobster, but the possibility that additional or alternative mechanisms exist in this and other species cannot be excluded.

Studies on magnetoreception in crustaceans are still at a very early stage. Given how few species and groups have been investigated so far, it appears possible that magnetoreception is a widespread sensory ability among crustaceans. Future studies in this area are likely to be rewarding.

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