

## MAGNETIC ORIENTATION OF SPINY LOBSTERS IN THE OCEAN: EXPERIMENTS WITH UNDERSEA COIL SYSTEMS

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### Summary

The western Atlantic spiny lobster *Panulirus argus* undergoes an annual migration and is also capable of homing to specific dens in its coral reef environment. Relatively little is known, however, about the orientation cues that lobsters use to guide their movements. To determine whether lobsters can orient to the earth's magnetic field, divers monitored the orientation of lobsters tethered inside magnetic coil systems submerged offshore in the Florida Keys, USA. Each coil could be used to reverse either the horizontal or vertical component of the earth's field.

Tethered lobsters walking inside the coils often established and maintained consistent courses towards specific directions. After a lobster had established a course, it was exposed to one of three conditions: (1) a reversal of the horizontal component of the earth's field; (2) a reversal

of the vertical component of the earth's field; or (3) no change in the ambient field (controls). Lobsters subjected to the horizontal field reversal deviated significantly from their initial courses. In contrast, control lobsters and those subjected to the reversed vertical field did not.

These results demonstrate that spiny lobsters possess a magnetic compass sense. Because inverting the vertical component of the earth's field had no effect on orientation, the results suggest that the lobster compass is based on field polarity and thus differs from the inclination compasses of birds and sea turtles. The magnetic compass of lobsters may function in homing behavior, in guiding the autumn migration or in both.

Key words: magnetic, orientation, magnetoreception, lobster, crustacean, invertebrate, *Panulirus argus*.

### Introduction

The western Atlantic spiny lobster *Panulirus argus* 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 lobsters within the same geographical area follow nearly identical compass bearings (Herrnkind *et al.* 1973), but the cues used by lobsters to maintain their migratory headings have not been determined. Field and laboratory experiments have demonstrated that 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). 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).

The ability to establish and maintain consistent courses is also an important component of spiny lobster behavior outside the migratory season. Between spring and early autumn, adult

lobsters typically spend the daylight hours inside coral reef crevices, emerging at night to forage within several hundred meters of the den (Clifton *et al.* 1970; Herrnkind *et al.* 1975). Before dawn, they return *via* a straight-line path either to the same den or to one of several others nearby (Herrnkind *et al.* 1975; Herrnkind and Redig, 1975). How lobsters can maintain consistent courses across variable terrain while returning to a home den in nearly total darkness has not been determined.

The earth's magnetic field provides a pervasive source of directional information that is used as an orientation cue by diverse animals (reviewed by Wiltschko, 1993). Among vertebrates, evidence exists for two functional types of magnetic compasses. Birds (Wiltschko and Wiltschko, 1972, 1988) and sea turtles (Light *et al.* 1993) appear to rely on an inclination compass that does not distinguish the polarity of field lines (i.e. north *versus* south); instead, an inclination compass functionally defines 'poleward' as the direction along the earth's surface in which the angle formed between the total

field vector and the gravity vector is smallest (Wiltschko and Wiltschko, 1972). For an animal with an inclination compass, inverting the vertical component of the ambient field has the same behavioral effect as reversing the horizontal component (Wiltschko and Wiltschko, 1988).

In contrast to inclination compasses, polarity compasses determine north using the polarity of the horizontal field component; thus, inverting the vertical field component does not alter the direction a polarity compass perceives as north (Wiltschko, 1993). Because reversing the vertical component does not affect the orientation of magnetically sensitive sockeye salmon (Quinn *et al.* 1981) and African mole rats (Marhold *et al.* 1991), these vertebrates are thought to possess polarity compasses.

Whereas the functional characteristics of several vertebrate magnetic compasses have now been investigated, comparable studies with invertebrates have never been conducted. We report that lobsters tethered under water in their natural habitat altered their direction of orientation when the horizontal component of the ambient magnetic field was reversed, but not when the vertical field component was inverted. These results provide evidence that lobsters have a magnetic compass based on field polarity.

## Materials and methods

### Study site

All experiments were conducted offshore near Key Largo, Florida, USA, during June 1992 and May 1993. The study site was Three Sisters Reef (latitude 25.03° N; longitude -80.40° W), located approximately 7 km from shore. The habitat consisted of an elongated patch reef occupying an area approximately 130 m long and 15–30 m wide, ringed by coral sand borders and surrounded by grass (*Thalassia testudinum*) beds that extended for several hundred meters in all directions. Major features of the underwater topography and the location of the underwater coils (see below) relative to the reef are shown in Fig. 1. The depth at the site where the coils were located was 6–7 m. All experiments were conducted during daylight hours (between 07:00 and 17:00 h).

### Animals

Juvenile and small adult lobsters (*Panulirus argus*; carapace lengths 45–77 mm) were located in holes and crevices throughout the patch reef by divers using SCUBA, prodded from their dens with thin fiberglass rods ('ticklesticks'), and captured in hand-held nets. Each animal was tested only once under one of the three experimental conditions (see below). Following testing, we noted the sex of each animal, measured its carapace length and identified distinguishing marks (e.g. missing appendages and scars), before releasing it on the reef. These recorded features enabled us to avoid testing any animal more than once.

### Eye caps and tethering

Once a lobster had been captured, divers quickly covered its

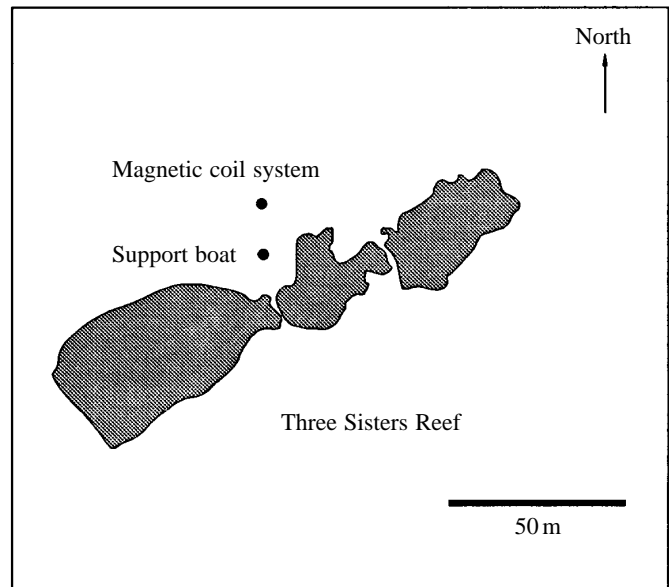


Fig. 1. Diagram of the Three Sisters Reef site, showing the outline of the reef, the location of the magnetic coils, and the position of the boat on which were situated the power supplies for the coil.

eyestalks with preformed rubber eye caps (Fig. 2) molded from polyvinylsiloxane impression material (Kerr Manufacturing Co.). Eye caps fitted snugly around the ommatidia that constitute the distal part of the eye and extended almost to the proximal base of the eyestalk. Lobsters fitted with eye caps and released in orientation arenas did not attempt to escape when divers approached closely, whereas lobsters with intact vision responded by backing away or tail-flipping. Thus, eye caps served the dual purposes of (i) temporarily depriving lobsters of visual cues that might be used in orientation and (ii) enabling divers to approach closely enough to monitor the lobsters' behavior.

Each eye-capped lobster was carried directly to an underwater arena approximately 25–75 m away from the capture site (Fig. 1). A plastic cable tie was wrapped around the lobster's cephalothorax between the fourth and fifth pairs of walking legs (Fig. 2). A small brass (non-magnetic) fishing tackle swivel threaded through the tie was arranged so that it was directly over the dorsal midline of the lobster. A monofilament line tied to the swivel was then attached to a polyvinylchloride (PVC) pipe support suspended above an acrylic walking surface (Fig. 3). Upon release, a lobster could therefore walk in any direction, but was restrained to a circle with a radius approximately equal to the length of the string.

### Orientation arenas

Orientation arenas consisted of squares (1.52 m each side) of transparent acrylic (1.27 cm thick). A circle 1.22 m in diameter was drawn on each square. Each circle was divided into 16 equal sectors marked by numbers that could easily be seen by a diver several meters away. All markings were made

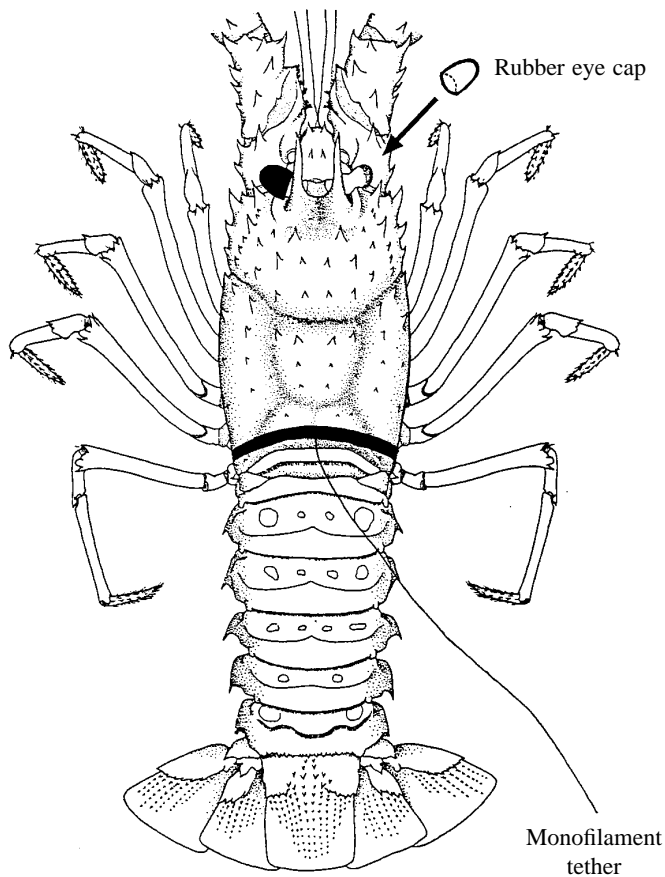


Fig. 2. Procedure for tethering lobsters. Rubber eye caps were placed over the eyes and eyestalks of each lobster to eliminate its vision. A plastic cable tie (indicated by the dark band) was then wrapped around the cephalothorax between the fourth and fifth pairs of walking legs. A monofilament line was attached to a small brass swivel (not shown) on the cable tie so that the lobster could be tethered to a support above an acrylic arena.

on the underside of the acrylic, so that lobsters walking on the surface could not contact the lines of indelible ink.

#### *Initial arena experiments*

In initial experiments, an arena was placed directly on the substratum (Fig. 3). To minimize possible slope cues, we adjusted the height of each corner of the acrylic square until a spirit level indicated that the surface was flat.

Ten lobsters were tested in initial trials. Each was fitted with eye caps, tethered and released on the acrylic surface. Once a lobster began to walk forward (see *Behavior of tethered lobsters* below), a diver moved into the water column several meters above the arena and monitored orientation for the next 20 min. At intervals of 2 min (for the first four lobsters) or 1 min (for the last six), a diver recorded the sector (1–16) in which the lobster walked. At the conclusion of each trial, these data were converted to angles (relative to magnetic north) and then used to calculate the mean angle and vector length ( $r$ ) for each lobster in accordance with standard procedures of circular statistics (Batschelet, 1981).

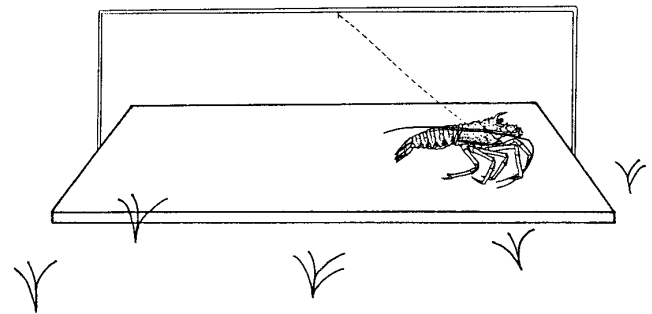


Fig. 3. Initial arena experiments in which acrylic squares were placed directly on the substratum. Lobsters were tethered to a PVC pipe support above the arena. See text for details.

#### *Reversing the horizontal field component*

In a second set of experiments, we constructed a magnetic coil system that could be used to reverse the horizontal component of the earth's field around lobsters tethered under water. The coil system consisted of four square wire coils all 2.0 m on each side arranged according to the design of Merritt *et al.* (1983). The supporting frame for the wire was constructed of PVC pipe (5.08 cm diameter). Electrical current to the coil was carried by a continuous length of insulated 16 gauge wire connected to a portable d.c.-regulated power supply in a boat moored a short distance (about 20–30 m) away. The coil could therefore be turned on or off from the surface.

The electrical current provided to the coil was adjusted so that the coil generated a magnetic field twice as strong as the horizontal component of the local geomagnetic field. Divers aligned the coil along the north–south axis so that the field it generated opposed the horizontal component of the earth's field. Thus, lobsters inside the coil could be exposed either to the natural geomagnetic field (when the coil was turned off) or to a magnetic field of equal intensity but with a reversed horizontal component. Magnetic field measurements were made on land with a Schonstedt single-axis digital fluxgate magnetometer (model DM 2220 R). Because the magnetic permeability of air and sea water are virtually identical, applying the same electrical current to the same coil in either medium presumably resulted in the same magnetic field. By placing a compass inside the coil, divers could confirm that the field was reversed when the power supply was activated.

An acrylic arena was placed on a plastic table inside the coil (Fig. 4). The height of the table was adjusted so that its surface was approximately halfway between the top and bottom of the coil. Thus, tethered lobsters walked in the area where the imposed field was most highly uniform (Kirschvink, 1992).

Because water currents and wave surge are known to influence lobster orientation under some conditions (Walton and Herrkind, 1977), the sides of the coil were wrapped with plastic sheeting to reduce possible hydrodynamic cues. The top remained open to provide divers with an unobstructed view of the tethered lobsters.

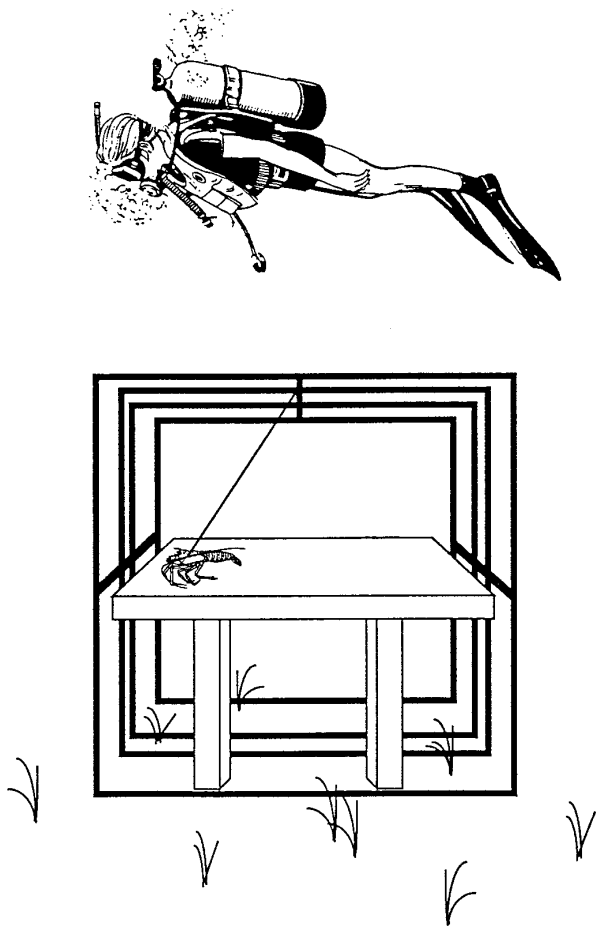


Fig. 4. Experiments in which lobsters were tethered inside underwater coil systems. A diver hovering in the water column above the coil monitored the orientation of each lobster. The plastic sheeting that surrounded the sides of the coil to diminish possible hydrodynamic cues is not shown.

#### *Reversed horizontal field trials*

Tethered lobsters wearing eye caps were released on the acrylic surface inside the coil. In approximately half of the trials, the coil was turned on and the field reversed before the lobster was introduced to the coil; in the remaining trials, lobsters began walking in the unaltered earth's field (coil turned off).

A diver stationed above the coil (Fig. 4) monitored the orientation of each lobster continuously. Headings were recorded at 1 min intervals, and any changes in course direction that occurred between these readings were also noted. A lobster was considered to have established a course when it had remained within any  $90^\circ$  sector for 5 min while walking steadily. Lobsters that failed to establish courses within about 40–60 min, or before divers had to return to the boat to replenish their air supplies, were replaced with other animals.

Once a lobster had established a course, a diver surfaced and signaled the boat crew. In response, the crew either (i) reversed the field by turning the coil on (if it was off) or off (if it was on), or (ii) did nothing, so that the field in which the lobster

was walking remained constant. The position of the lobster was then recorded at 1 min intervals for the next 5 min.

#### *Reversing the vertical field component*

A second coil system was constructed to reverse the vertical component of the earth's field. This coil was based on a Helmholtz design and consisted of two square coils (229 cm each side), each consisting of 40 wraps of 18 gauge insulated wire. When connected to a d.c. power supply, the coil produced a magnetic field twice as strong as the local geomagnetic vertical component and in the opposite direction (i.e. straight up). Thus, activating the coil reversed the direction of the vertical field component without altering the horizontal component. As with the first coil, an acrylic arena was placed in the center, and the periphery of the coil was wrapped with plastic sheeting to diminish possible hydrodynamic cues.

Lobsters were captured and treated as before, except that all trials began with a lobster walking in the earth's field (with the coil turned off). Once a lobster had established and maintained a course for 5 min, it was either (i) exposed to a reversal of the vertical field component, or (ii) allowed to continue walking in the unaltered magnetic field of the earth. In each case, the orientation of the lobster was monitored for an additional 5 min after the baseline period.

#### *Analysis of coil experiments*

A lobster was considered to have established a course when it had walked within a  $90^\circ$  sector for 5 min (see above). Using standard procedures for circular statistics (Batschelet, 1981), we calculated a mean baseline angle for each individual based on the six consecutive 1 min readings during this period (time=0, 1, 2, 3, 4 and 5 min).

Because different lobsters walked towards different directions during the baseline period (see Results), each lobster's mean baseline angle was normalized to  $0^\circ$ , and all subsequent orientation was plotted relative to this initial heading. This procedure enabled us easily to compare responses of lobsters to the different magnetic treatments by determining whether animals maintained their original courses or changed direction in each case.

As a simple measure of whether lobsters maintained or changed course during the 5 min following the baseline period, we recorded the maximum deviation of each lobster from its mean baseline angle. This measure represented the largest change in heading from the initial direction and was plotted on a circle relative to the normalized baseline angle of  $0^\circ$ . Thus, an animal that did not deviate at all from its initial course would have had a maximum deviation of  $0^\circ$ , whereas one that reversed course and walked in the opposite direction would have had a maximum deviation of  $180^\circ$  (see Results).

The data were analyzed using standard procedures for circular statistics (Batschelet, 1981) to determine (1) whether each distribution was significantly different from random, and (2) whether deviations of lobsters subjected to horizontal or vertical field reversals were significantly different from those of control lobsters.

## Results

### Behavior of tethered lobsters

When released onto an acrylic surface, most tethered lobsters tail-flipped or backed away from the site of release, then turned and began to walk forwards. No discernible change in behavior occurred at the moment when the tether became taut; instead, animals continued to walk at the same steady rate with their legs slipping continuously across the acrylic surface. Forward walking was occasionally interrupted by brief pauses (usually 3–10 s), but was otherwise continuous for the duration of the various trials.

### Initial arena experiments

In initial arena experiments, tethered lobsters wearing eye caps often established relatively consistent courses and maintained them for periods of several minutes (Fig. 5). Whereas some individuals adopted steady courses almost immediately after release, others did not do so until several minutes later, and a few changed direction almost continuously throughout the entire test period. These differences are reflected in the varying vector lengths ( $r$  values) for different animals (Fig. 5A). Although exceptions existed, the courses of lobsters during the last 10 min of the trial were usually slightly more consistent (mean individual  $r$  values of 10 lobsters=0.64; Fig. 5B) than the courses over the first 10 min (mean  $r$ =0.50; data not shown) or the entire trial (mean  $r$ =0.49; Fig. 5A).

Different lobsters walked towards different directions (Fig. 5). The lobsters were not significantly oriented as a group during the first 10 min [ $F(2,8)=2.37$ ,  $P>0.20$ , Hotelling test], during the last 10 min [ $F(2,8)=0.04$ ,  $P>0.50$ , Hotelling test] or for the entire 20 min trial [ $F(2,8)=0.29$ ,  $P>0.20$ , Hotelling test].

During these short experiments, several lobsters maintained

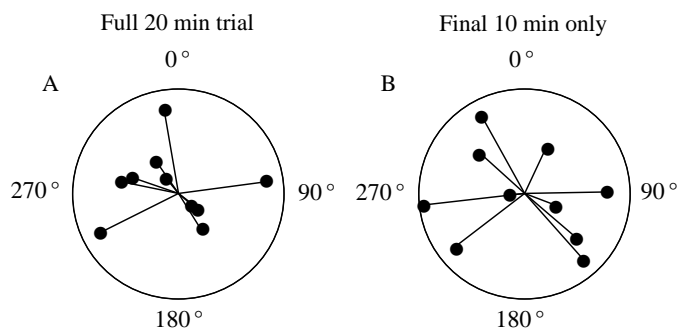


Fig. 5. Results of orientation experiments in which lobsters were tethered on acrylic squares placed directly on the substratum (as shown in Fig. 3). The length of each line is proportional to the mean vector length, with a line reaching the edge of the circle corresponding to  $r=1$  (Batschelet, 1981). Long lines thus indicate consistent orientation towards the same direction throughout the test period; shorter lines indicate greater directional variability. (A) Results using all bearings for 10 lobsters recorded during each 20 min trial. Although several lobsters held relatively consistent courses, no significant directional preference existed for the group (see text for statistics and details). (B) Results using only the bearings recorded during the last 10 min of each 20 min trial. As in A, no significant directional preference existed for the group (see text for details).

highly consistent courses for periods of 10 min or longer. Three such sequences (each from a different lobster) are shown in Fig. 6. These results suggested that once an individual had walked within a  $90^\circ$  range for five consecutive minutes, it was likely to maintain a very similar course during the next 5 min period. This observation provided the basis of the procedures developed for use in subsequent magnetic orientation experiments.

### Magnetic orientation experiments

Control trials were conducted with lobsters tethered under three conditions: (i) within the horizontal coil, with the coil off for the entire trial; (ii) within the horizontal coil, with the coil on for the entire trial; (iii) within the vertical coil, with the coil off for the entire trial. No statistical differences in responses could be discerned between the three groups; thus, all control trials were grouped together ( $N=14$  total).

During control trials, lobsters adopted initial courses towards seemingly random directions, as those tested in the initial arena trials (Figs 3, 5) had done. The baseline directions chosen by lobsters inside the coils were statistically indistinguishable from random (data not shown), regardless of whether the bearings were plotted relative to true geomagnetic north (i.e. without regard to whether the field was reversed or not) or magnetic north within the coil.

Although different individuals walked in different directions, lobsters in control trials deviated relatively little from their initial courses during the 5 min following the baseline period (Figs 7, 8). In contrast, most lobsters subjected to a reversal of the horizontal field component adopted new

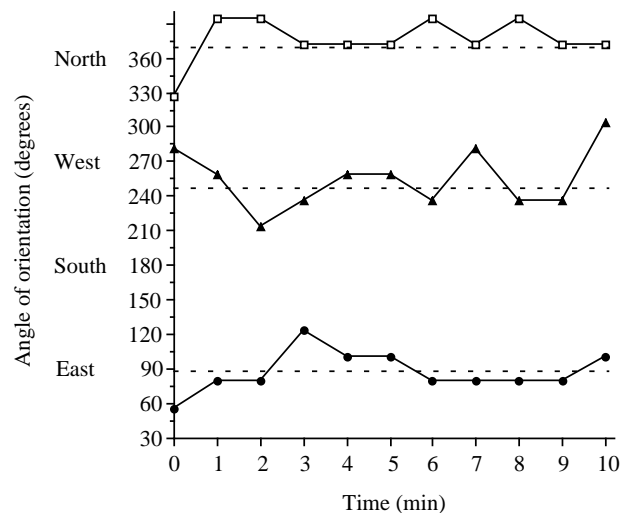


Fig. 6. Orientation of three different tethered lobsters with highly consistent bearings. The headings of each individual are indicated by different symbols (squares, triangles or circles). Time is indicated along the horizontal axis and the heading of the lobster is indicated along the vertical axis. Dotted lines represent the mean angle of orientation for each lobster during the first 5 min that it walked within a  $90^\circ$  sector (time 0–5 min). During the next 5 min, lobsters maintained courses similar to those that they had established during the first 5 min.

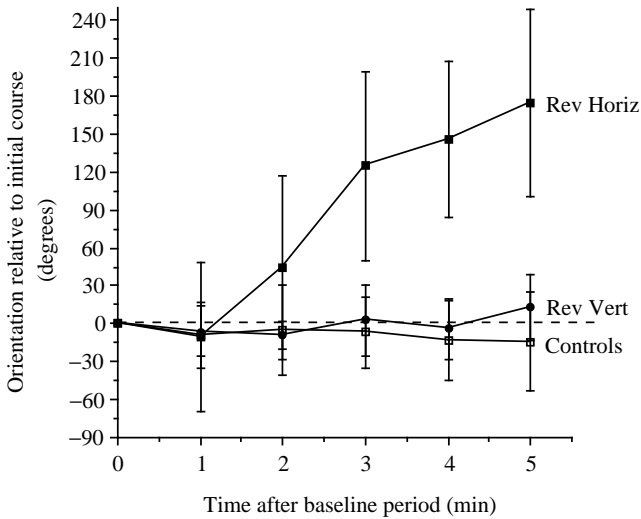


Fig. 7. Orientation of lobsters as a function of time after the baseline period. Open squares (Controls) represent the mean angles of the control lobsters ( $N=14$ ), filled squares (Rev Horiz) indicate the mean angles of lobsters subjected to a reversed horizontal field ( $N=9$ ), and filled circles (Rev Vert) indicate the mean angles of lobsters tested in reversed vertical field trials ( $N=9$ ). The dotted line at  $0^\circ$  indicates the normalized baseline angle (see text). Thus, lobsters that did not deviate at all from their baseline courses remained at  $0^\circ$  for the duration of the trial. Error bars indicate angular deviation, the equivalent of standard deviation in circular statistics (Batschelet, 1981). In control trials and reversed vertical trials, lobsters never deviated significantly from their initial baseline courses. In contrast, the orientation of lobsters subjected to a reversal of the horizontal field began to diverge from controls approximately 2–3 min after the field was reversed. The orientation of these two groups was significantly different at 3 min ( $U^2=0.354$ ,  $P<0.002$ , Watson test), 4 min ( $U^2=0.329$ ,  $P<0.002$ ) and 5 min ( $U^2=0.258$ ,  $P<0.01$ ). Orientation of control lobsters never differed significantly from that of lobsters subjected to the reversed vertical field.

headings considerably different from their original directions (Figs 7, 8). The bearings of lobsters subjected to the horizontal

field reversal began to diverge from those of controls about 2 min after the field had been altered (Fig. 7); the headings of the two groups were significantly different by 3 min ( $U^2=0.354$ ,  $P<0.002$ , Watson test), and the mean courses diverged still farther as the testing period progressed (Fig. 7).

An analysis of maximum course deviations produced similar results (Fig. 8). The distribution of maximum deviation angles for control lobsters (Fig. 8, left) was significantly non-uniform ( $r=0.55$ ,  $Z=4.31$ ,  $P=0.012$ , Rayleigh test) and had a mean angle of  $350^\circ$ , only  $10^\circ$  from the normalized baseline angle of  $0^\circ$ . The distribution for lobsters tested in the reversed horizontal field was also non-uniform ( $r=0.69$ ,  $Z=4.36$ ,  $P<0.01$ , Rayleigh test), but with a mean angle of  $183^\circ$  (Fig. 8, middle). These two distributions are significantly different ( $U^2=0.378$ ,  $P<0.001$ , Watson test). Thus, the ambient magnetic field influenced the orientation of spiny lobsters under the experimental conditions.

In contrast to results obtained when the horizontal field was reversed, lobsters did not deviate significantly from their initial courses when the vertical component of the field was inverted (Fig. 7). The distribution of maximum deviations for lobsters in the reversed vertical field group was significantly non-uniform ( $r=0.61$ ,  $Z=3.43$ ,  $P<0.035$ ) and had a mean angle of  $3^\circ$  (Fig. 8, right). This distribution, however, did not differ significantly from that of control lobsters ( $U^2=0.0621$ ,  $P>0.50$ , Watson test).

### Discussion

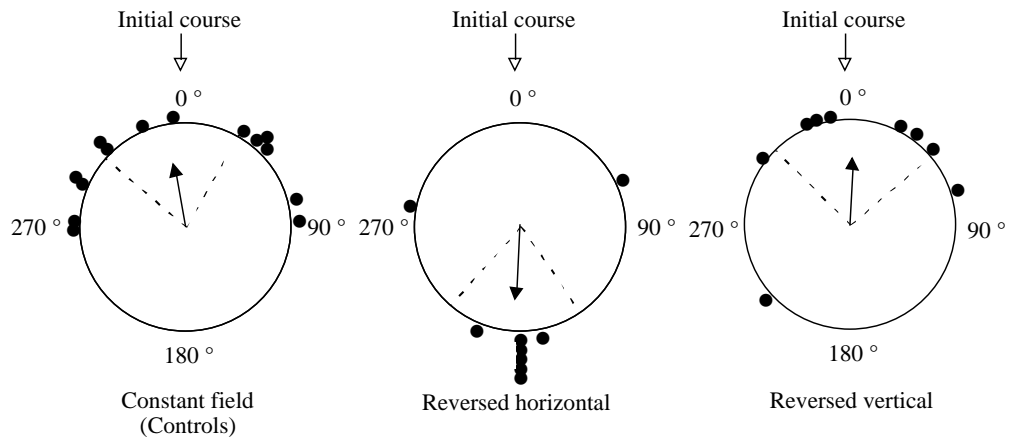
#### Magnetic compass orientation

Lobsters subjected to a reversal of the horizontal field usually altered course considerably within a few minutes after the field change, whereas control lobsters tested in a constant field did not (Figs 7, 8). We infer that lobsters can detect the geomagnetic field and use it as a cue in orientation.

#### Previous studies on lobster magnetic orientation

In an earlier field experiment, Walton and Herrnkind (1977) attached either magnets or non-magnetic solder wire to non-

Fig. 8. Maximum deviations of lobsters relative to the normalized baseline angles of  $0^\circ$  (see text). Each data point represents one lobster. Lobsters that did not deviate at all from their baseline courses had maximum deviations of  $0^\circ$ , whereas those that reversed course fully had deviations of  $180^\circ$ . A deviation of  $90^\circ$  indicated that the lobster shifted  $90^\circ$  clockwise from its initial course;  $270^\circ$  indicated that the lobster shifted  $90^\circ$  counterclockwise, and so on. Arrows 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 (Batschelet, 1981). Left: results from control lobsters. Middle: results from lobsters subjected to a reversal of the horizontal field component. Right: results from lobsters subjected to a reversal of the vertical field component. See text for analysis and statistics.



injuriously blinded adult spiny lobsters, then released them outside their home range in an area with considerable wave surge (horizontal displacements of about 10–50 cm). Under these conditions, both groups of lobsters oriented into the surge, and no difference in behavior between control lobsters and those bearing magnets could be discerned.

Conditions in our present study differed in that tethered lobsters were tested when wave surge was minimal or absent. In addition, we used coil systems that produced relatively uniform earth-strength magnetic fields around the lobster, rather than attempting to distort or obscure the earth's field with the stronger field of a bar magnet. Under these conditions, the ambient field influenced orientation (Figs 7, 8).

Weak evidence for magnetic sensitivity in spiny lobsters was previously reported from laboratory experiments in which attempts were made to condition animals to move into tunnels aligned with specific magnetic directions (Lohmann, 1985). The results of the present study are consistent with the initial report and also suggest that manipulating the field around spontaneously orienting lobsters provides a better approach to studying magnetic orientation in these animals.

#### *Evidence for a polarity compass*

Among vertebrate animals, evidence has been reported for two distinct types of magnetic compasses, one based on field line inclination and the other on field polarity (reviewed by Wiltschko, 1993). The two compass types can be distinguished by inverting the vertical component of the field. For animals with inclination compasses, this manipulation has the same effect as reversing the horizontal field; it has no effect, however, on the orientation of animals with polarity compasses. Because lobsters subjected to a reversal of the vertical field component did not alter course significantly (Figs 7, 8), the results are consistent with the hypothesis that the magnetic compass of lobsters is based on field polarity.

To our knowledge, the only other attempt to investigate the functional characteristics of an invertebrate magnetic compass was carried out by Arendse (1978), who reported that the flour beetle *Tenebrio molitor* was able to orient magnetically in an earth-strength horizontal field. Because animals with an inclination compass are unable to orient magnetically under this condition (Wiltschko and Wiltschko, 1972; Light *et al.* 1993), these results suggest that flour beetles, like lobsters, may have a polarity compass. Whether polarity compasses are widespread among arthropods and other invertebrates, however, remains to be determined.

#### *Magnetic orientation and movement patterns of lobsters*

Although individual lobsters often maintained consistent courses in our experiments, different individuals walked towards different directions (Figs 5, 6). The data thus provided no support for the hypotheses that the lobsters were attempting to home to the patch reef, orient offshore or otherwise move in a common direction. Instead, each lobster appeared to walk in a direction of its own choosing, which had no apparent relationship to the directions chosen by others.

On the basis of carapace length, the lobsters used in our study were all juveniles and young adults. Thus, the random directions observed in our study are consistent with the apparently random dispersal of similar lobsters tagged and released in the Florida Keys and Cuba (Dawson and Idyll, 1951; Buesa Mas, 1965). Other studies have also provided evidence that immature and young adult lobsters are more transient and less residential than older, mature individuals (Olsen *et al.* 1975; Davis, 1977).

In contrast to the tethered lobsters in the present study, lobsters captured on the same patch reef and released from two sites nearby consistently walked offshore (for at least 20 min) in a direction correlated with wave surge (Nevitt *et al.* 1995). Because wave surge was minimal or absent during days when tethering experiments were conducted, one possibility is that the apparent differences in orientation between unrestrained and tethered lobsters might have been attributable to differences in the availability of hydrodynamic cues.

In principle, magnetic compass orientation might play a role in guiding movements of both juvenile and adult lobsters. Juveniles appear to maintain relatively consistent headings over considerable distances during their nomadic wanderings, and adults maintain straight-line paths when homing to dens following their nightly foraging trips (Herrnkind, 1980). The magnetic compass might also function in guiding lobsters offshore during their annual migration, when hydrodynamic cues frequently provide little consistent directional information and visual cues are often absent (Herrnkind, 1985).

#### *Mechanism of magnetic field detection*

The mechanism(s) underlying magnetic field detection have not been clearly established in any multicellular organism. Although numerous hypotheses of magnetoreception have been proposed, direct neurobiological evidence has not yet been obtained for any of them (reviewed by Lohmann, 1996).

One hypothesis proposes that particles of the mineral magnetite provide the physical basis for the magnetic sense (Kirschvink and Gould, 1981; Kirschvink, 1982, 1989). Magnetic material (possibly magnetite) has been detected in the cephalothorax of the western Atlantic spiny lobster (Lohmann, 1984), as well as in a number of other animals known to orient magnetically (Kirschvink *et al.* 1985). In lobsters, the direction of the natural remanent magnetization in different parts of the cephalothorax is relatively consistent from individual to individual, suggesting that the particles are aligned in a similar way within each animal (Lohmann, 1984). Such an array of magnetic particles might, in principle, function in transducing geomagnetic cues to the nervous system. Alternative transduction mechanisms, however, cannot presently be ruled out.

A related question that cannot yet be addressed is whether polarity and inclination compasses are based on different transduction mechanisms. One possibility is that the different functional characteristics of each compass type directly reflect properties intrinsic to different underlying receptors. Alternatively, however, differences in compass function might

arise from variations in higher-order neural processing. Such variations could result in different behavioral outputs despite similar input from identical receptors.

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