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EVIDENCE FOR HYDRODYNAMIC ORIENTATION BY SPINY LOBSTERS IN A PATCH REEF ENVIRONMENT

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Summary

Western Atlantic spiny lobsters (*Panulirus argus*) are superb underwater navigators. Spiny lobsters perform dramatic seasonal offshore migrations and have also been shown to locate and home to specific den sites within the elaborate coral reef environment in which they live. How these animals perform such complex orientation tasks is not known. The study reported here was designed to explore the sensory mechanisms that spiny lobsters use to orient in and around a familiar patch reef environment. Our results show that, in the absence of visual cues, lobsters displaced a short (50 m) distance off the reef do not initially (i.e. within 20 min) travel towards their dens or return to the patch reef where their dens are located. Instead, the headings lobsters follow are significantly correlated to the direction of local hydrodynamic cues and, specifically, to the direction of approaching wave surge. Results from ultrasonic tracking experiments over longer periods (24 h) suggest that displaced lobsters are able to relocate the reef where they were captured, even without visual cues. These results suggest that hydrodynamic cues may provide useful and immediate directional information to lobsters within the local environment of the home reef.

Key words: *Panulirus argus*, orientation, Homing, navigation.

Introduction

Spiny lobsters (*Panulirus argus*) are known for their ability to find their way accurately in and around the complex environment of the coral reef. In addition to their dramatic seasonal offshore migrations, adult spiny lobsters have been shown to possess a sophisticated homing sense which allows them to relocate their dens within the often elaborate maze of the reef infrastructure (reviewed by Herrnkind, 1980). Spiny lobsters typically inhabit one of several home dens in reef crevices and holes, either alone or in groups (Herrnkind *et al.* 1975). Lobsters remain within these refuges throughout the daylight hours, but emerge after sunset to forage within several hundred meters of their den (Clifton *et al.* 1970). Before dawn, they home either to the same den or to one of several others nearby (Herrnkind and Redig, 1975).

The ability of spiny lobsters to home has been well documented, but how they are able to perform this complex behavior is not well understood. Spiny lobsters have repeatedly been shown to return accurately to an area of capture, even after forced displacement outside the home range (Creaser and Travis, 1950; Herrnkind and McLean, 1971). However, blindfolded spiny lobsters released well outside the home range do not initially orient towards home, but instead head offshore, apparently guided by hydrodynamic cues (i.e. incoming wave surge and water currents; Herrnkind and McLean, 1971; Walton and Herrnkind, 1977). It has been speculated that part of this response may be stress-induced: a spiny lobster displaced far from its home range may use a general set of hydrodynamic cues to orient offshore to the relative safety of deeper water (Herrnkind, 1980). What potential guideposts spiny lobsters use to orient when they are displaced close to their dens have not been examined.

The study reported here was designed to examine the sensory mechanisms that spiny lobsters use to orient in and around the local environment of a familiar patch reef. To begin this investigation, we first tested whether blindfolded spiny lobsters displaced a short (50 m) distance from the reef would initially orient back to a particular den of capture. We found this not to be the case: instead of heading in the direction of the den site and traversing the relatively short distance to get there, displaced blindfolded lobsters chose headings more tightly aligned to the direction of approaching wave surge. Blindfolded lobsters tracked over longer periods always returned to the reef of capture within 24 h after release, demonstrating that their initial tendency to head offshore did not necessarily reflect long-term movement patterns or an inability to relocate the reef. These results are consistent with the hypothesis that hydrodynamic cues provide primary and immediate directional information to displaced spiny lobsters, even in the familiar territory around the den site.

Materials and methods

Study site

Experiments were conducted during June 1992 in the immediate vicinity of the Three Sisters Patch Reef located 10 km southeast of Key Largo, Florida (Fig. 1). Three Sisters Patch Reef was selected as a study site because it is a relatively isolated reef surrounded by open sand and grass beds. The nearest neighboring patch reef is approximately 0.5 km away. Three Sisters Patch Reef thus provided the most extensive lobster habitat in the immediate area, presumably making it the preferred homing target for displaced residential spiny lobsters. Maximum depth at this site was 6 m.

Initial orientation behavior

Spiny lobsters (42–72 mm carapace length) were captured from dens by divers using SCUBA. Lobsters were gently prodded from their dens with thin fiberglass rods and captured using hand-held nets. Each lobster was kept at depth and blindfolded under water by covering the eyes with opaque caps previously custom-fabricated from a non-toxic dental impression material (polyvinylsiloxane, Kerr Manufacturing Co.). Once an experimental run had been completed, eye caps were easily removed without injury, and the lobster was marked and released.

To begin an experimental run, one diver gently hand-carried the eye-capped lobster to one of two grass bed release sites located 50 m away from the area of capture (see Fig. 1). A second diver marked the lobster's den (designated as the 'home' den; Herrnkind and Redig, 1975) and strung a measuring tape between it and the release site. Divers could thus use this line as a guide for an accurate compass bearing to the den's position from the release site. The lobster was then placed on the ground facing one of four compass headings (0 °, 90 °, 180 °, 270 °). Release headings were varied by 90 ° increments between successive lobsters. After the lobster had been released and had walked a meter or so, the exact location of release was marked with a fiberglass rod. The progress of the lobster was monitored by a pair of divers hovering above and several meters to one side of the lobster.

At 2 min intervals over a period of 20 min, the lobster's cephalothorax compass bearing, locomotory behavior (walking or not walking) and distance from the release site were noted. Detailed behavioral observations were recorded only at these intervals. At the end of the 20 min trial, a tape measure was strung between the release point and the final position of the lobster. The lobster's final heading relative to the release site was determined by taking a compass bearing along this line. The carapace length and sex of each lobster were recorded, and each lobster was used only once. After each trial, the direction

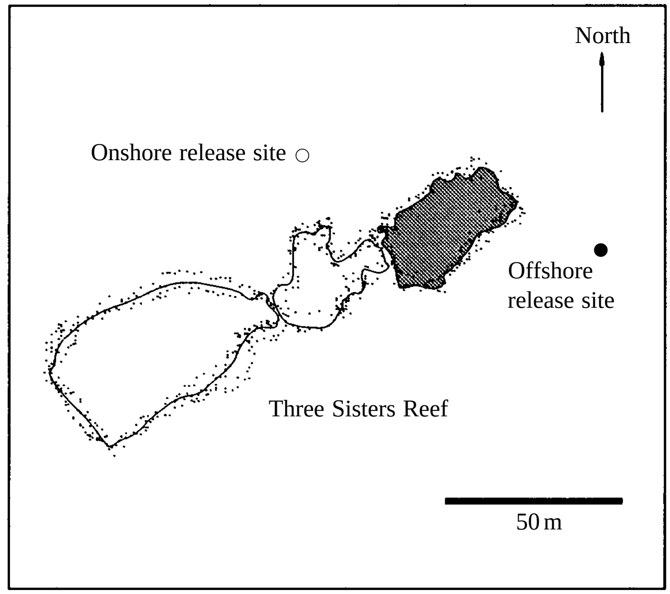

Fig. 1. Three Sisters Patch Reef and vicinity (25° 01′ 46.348″ N, 80° 23′ 53.813″ W). The reef outlines (small dots) were mapped using a differential GPS receiver (see Materials and methods). Lobsters used in experiments were captured from dens located in the shaded area. The two release sites are indicated (offshore, filled circle; onshore, open circle).

of approaching wave surge was determined by observing the movement of fluorescein dye traces 1.5 m above the substratum; the velocity and direction of the local water current were measured by timing the movement of dye traces released from a height of 30 cm.

Long-distance tracking using ultrasonic transmitters

Lobsters were tracked with ultrasonic transmitters over longer times and distances than were possible using SCUBA. Sample sizes of tracked animals were limited owing to technical constraints in following multiple individuals for several days in the field. In order to distinguish animals, transmitters (Sonotronics Co.) were tuned to different 'ping' rates and carrier frequencies. Carrier frequencies were set at 32.7 kHz or 40 kHz and were detectable for as far as 0.5 km over open eelgrass beds. Over the course of 3 days (15–18 June 1992), six lobsters were captured and eye-capped using the techniques described above. Each eye-capped lobster was transported to a holding tank located on the support boat. Each animal was removed briefly from the tank, and a transmitter, which had been previously glued to a small neoprene pad, was attached to the dorsal side of the cephalothorax with cyanoacrylic glue. Lobsters were returned to the holding tank and then transported individually to one of the two release sites used in the previous set of experiments (three at each site, Fig. 1). Each lobster was released and visually tracked under water by SCUBA divers for up to 20 min, following the same protocols described above. The position of each lobster was periodically monitored for at least 2 days following release using a surface-operated receiver and directional hydrophone.

In cases where multiple directional bearings were needed to triangulate a lobster's position, the receiver's position was determined using a differential global positioning system (GPS, Trimble Pathfinder Professional). After 2–3 days, lobsters that could be recaptured were brought to the surface, where eye caps and transmitters were removed. Lobsters were then gently carried back to the reef and released.

Statistical analysis

The final headings (i.e. the direction of net displacement from the release site) taken by lobsters were first analyzed for non-uniform distribution using the Rayleigh test (Batschelet, 1981). We then examined whether a suite of possible orientation cues was correlated to these headings. Potential cues tested were as follows: (1) the location of the home den, (2) the initial orientation imposed at release, (3) the direction of the local water current movement, and (4) the direction of approaching wave surge.

We extended this analysis to the subset of lobsters that followed the straightest trajectories. We first determined an 'index of straightness' of each lobster's trajectory by vector-averaging 2 min bearings for each lobster. For this analysis, we only included bearings recorded while animals were walking. A significance level could not be assigned to the calculated mean vectors since each 2 min bearing could not be considered as an independent data point (Batchelet, 1981). We consequently designated the 'straightest' lobsters as those walking paths having a mean vector length (i.e. **r** value) of 0.50 or greater (see Emlen and Demong, 1978; Batchelet, 1981). We next examined what influence potential orientation cues had on these lobsters using the same criteria outlined above.

All data are presented as circular diagrams with headings and mean bearings normalized to zero. Means are presented as ± one standard error. Significance levels (*P*-values) are corrected appropriately for multiple comparisons.

Results

General observations

Upon release, eye-capped lobsters showed no obvious reaction to the presence of divers in the vicinity. At 4 min, 18 out of 19 animals tested had begun to walk and had assumed a regular, though slow (up to 5 cm s^{-1}), pace compared with walking velocities reported in other studies (i.e. 16 cm s^{-1} for adult lobsters walking on sand; Herrnkind and McLean, 1971). In all but one trial, lobsters consistently travelled forward, but occasionally stopped (2.9±0.4 stops per lobster as recorded at the 2 min observation points). Lobsters tended to zigzag along a specified heading for some part of the observation period, but variations in this behavior were also observed. For example, in four instances, lobsters did not zigzag, but travelled in broad circular paths; backtracking along a previously used path was observed in two other trials. On two occasions, lobsters veered off a directed course towards small coral heads or other isolated areas of shelter.

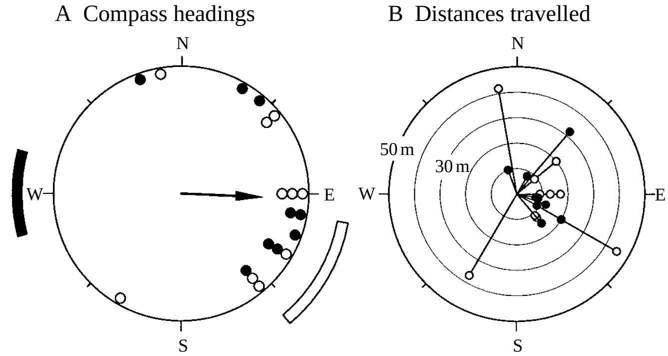

Fig. 2. (A) Final headings (i.e. direction of net displacement after 20 min) of eye-capped lobsters released 50 m from the home reef at the onshore site or the offshore site (see Fig. 1). Each symbol indicates the final heading of an individual lobster. Open circles denote headings taken by lobsters released from the onshore site, while filled circles denote headings taken by lobsters released from the offshore site; the direction of home for lobsters released from the onshore site is denoted by the open bar. The direction of home for lobsters released from the offshore site is denoted by a filled bar. The arrow denotes the mean angle of orientation for all lobsters tested. The length of the arrow is proportional to the mean vector of orientation or **r** value (Batchelet, 1981; an **r** value of 1.0 indicates that there is no dispersion in the data). (B) Distances travelled by lobsters over the course of 20 min. Lines topped with open circles indicate distances travelled by lobsters released from the onshore site; lines topped with filled circles indicate distances travelled by lobsters released from the offshore site.

Visual tracking

Upon release from the onshore site, the absolute distance individual lobsters travelled varied considerably (Fig. 2B), but animals consistently progressed in the direction of their home dens (Fig. 2A, open circles). The mean angle of orientation for the onshore release group was significantly non-random (96 °, N=10; **r**=0.60; Z=3.65; P<0.05). When released from the offshore site, however, lobsters failed to orient towards their dens or the home reef. Instead, they oriented in the same direction as lobsters released from the onshore site (Fig. 3A, filled circles; mean angle of orientation 90 °, N=9; **r**=0.67; Z=4.11; P<0.05). The final orientation of the combined sample population was highly non-random (N=19; **r**=0.63; Z=7.71; P<0.005). Distances travelled were also similar between lobsters released from either site (Fig. 2B). From the combined data, we conclude that lobsters released in close proximity to their dens did not orient towards home, but oriented instead to a common easterly compass direction.

To determine the other external factors that may have influenced their orientation choices, we analyzed the final headings of lobsters relative to four potential directional influences, including the direction of (1) release, (2) home, (3) prevailing water currents and (4) approaching wave surge. The results of this analysis are shown in Fig. 3. Final headings were more strongly correlated to the direction of approaching wave surge (**r**=0.54, Z=6.47; P<0.05) than to the any of the other guideposts tested, including the direction of the home den (**r**=0.15, Z=0.47; P>0.10). Contrary to earlier work (Herrnkind

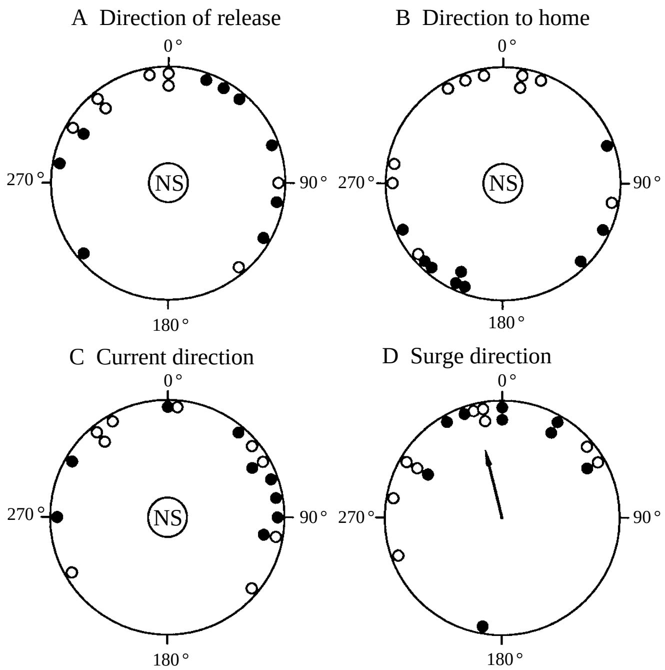

Fig. 3. Final headings of eye-capped lobsters displaced from Three Sisters reef relative to four potential orientation cues: (A) direction of release; (B) direction to home; (C) current direction; (D) surge direction. Open circles denote the final headings of lobsters released from the onshore site; filled circles denote the final headings of lobsters released from the offshore site. Headings are normalized such that the direction of the environmental cue is always at 0˚; each lobster's final heading is thus expressed as a deviation from 0˚. The arrow denotes the mean angle of orientation for both groups of lobsters combined, and the length of the arrow is proportional to the mean vector of orientation or **r** value. NS in the center of the plot indicates that the combined mean orientation is not significantly different from random by a Rayleigh's test (P>0.05).

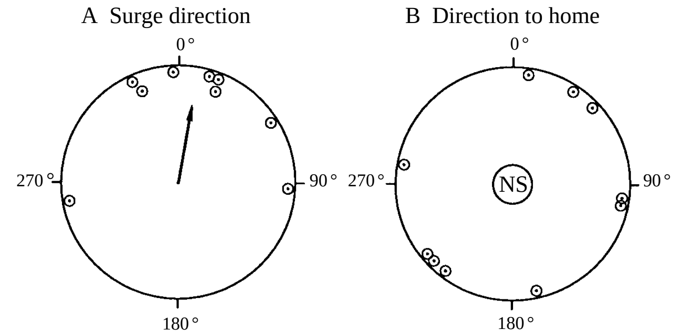

Fig. 4. Mean bearings of the subset of eye-capped lobsters showing the highest straight-line orientation (**r**>0.5) relative to (A) surge direction and (B) direction to home. As in Fig. 3, bearings are normalized such that the direction of the environmental cue is always at 0˚; each lobster's bearing is thus expressed as a deviation from 0˚. The arrow denotes the mean angle of orientation for all animals in this group, and the length of the arrow is proportional to the **r** value. NS in the center of the plot indicates that the combined mean orientation is not significantly different from random by a Rayleigh's test (P>0.05).

and McLean, 1971), we found that eye-capped lobsters were not influenced by the experimental bias imposed on them at release (**r**=0.38, Z=2.55; P>0.10) or the direction of local water currents (**r**=0.42, Z=3.28; P>0.05). Eye-capped lobsters also responded similarly to external cues regardless of sex or size (data not shown).

Some lobsters appeared to 'beeline' more than others (**r**>0.50; see Materials and methods), giving an impression that they were deliberately heading in a specific direction, such as that of the home den (Herrnkind and Redig, 1975). This subset of lobsters established a course soon upon release (Fig. 4) and their orientation coincided strongly with the direction of approaching wave surge (Fig. 4A, **r**=0.67; Z=4.07; P<0.05). Mean bearings were not correlated to the location of the home den (Fig. 4B, **r**=0.09, Z=0.08; P>0.10), the direction of release (**r**=0.33, Z=1.14; P>0.10) or current direction (**r**=0.41, Z=1.75; P>0.10).

Ultrasonic tracking

The results described above suggest that, in the absence of visual cues, displaced spiny lobsters do not initially orient back to their dens, even when released in the immediate vicinity of their local reef. To test whether eye-capped lobsters were capable of relocating the reef over longer periods than we could observe with SCUBA, the movements of six blindfolded lobsters were monitored over several days using telemetry (see Materials and methods). All six ultrasonically tracked eye-capped lobsters reappeared within meters of their original capture sites within the first 24 h following release. Interestingly, within 3 days, two of these lobsters eventually moved 0.5–1.0 km offshore and were not seen again on the reef. Both of these animals were released from the onshore release site.

Discussion

The purpose of this study was to investigate the sensory information that spiny lobsters use to orient in a familiar patch reef habitat in the context of relocating the home den. Our current investigation thus extends earlier work (Herrnkind and McLean, 1971; Walton and Herrnkind, 1977) examining the long-distance homing abilities of lobsters in that our experiments were performed very close to where animals were residing. In addition, we focused our efforts on tracking individuals in detail over a 20 min period rather than measuring the consistencies of vanishing bearings over repeated releases. Finally, judging by the size range of the populations studied (Hunt and Lyons, 1986), many lobsters tested in the present study were probably juveniles or sub-adults, whereas earlier work has focused almost exclusively on homing behavior in adults (reviewed by Herrnkind, 1980). Details are described below.

Lack of initial home den orientation

We found that eye-capped lobsters released from an onshore site oriented in the direction of the reef. However, a second group of eye-capped lobsters released this time from an offshore site consistently oriented along the same compass headings as those released from the first site. In short, eye-capped lobsters consistently oriented in an easterly direction offshore rather than in the direction of the home den, even when displaced in the vicinity of the home reef (Fig. 2A).

The absence of initial home den orientation is consistent with data reported from studies examining orientation in lobsters displaced much greater distances outside the home range. Herrnkind and McLean (1971) showed that neither sighted nor blindfolded lobsters consistently oriented towards home when tested 2–5 km from their home dens. Experiments by the same authors using acoustically tagged lobsters showed, however, that adults could eventually return home from these distances. Results from our telemetry experiments similarly suggest that eye-capped lobsters are able to relocate the 'home' reef following displacement over short distances, but that this behavior is not reflected in their initial headings. The picture that emerges is that displaced lobsters can eventually relocate familiar dens, but that they first orient offshore, regardless of the familiarity of the terrain or the absolute distance from home.

It is also plausible, however, that once displaced, lobsters lose motivation to return to the site of capture, regardless of whether or not they are capable of relocating home. Disturbance could even provoke them to abandon an area altogether (Herrnkind, 1980), as apparently occurred in two of the six acoustically tagged lobsters between 48 and 72 h after release. Neither this study nor earlier work (Herrnkind and McLean, 1971; Walton and Herrnkind, 1977) documents long-term residency patterns of the individuals in the populations studied. We did, however, routinely note the recapture of specific individuals over the course of this investigation, confirming that many individuals had remained in the immediate area even after having been forcibly displaced. A potentially confounding issue is that spiny lobsters sometimes occupy multiple dens (reviewed by Herrnkind, 1980). We do not think that this behavior affected our results since lobster dens were well concentrated on the patch reef relative to either release site (Fig. 2A). Displaced lobsters walking towards any den were consequently obliged to orient in a similar direction relative to home regardless of the precise location of the home den.

Hydrodynamic influences

The results presented here suggest that the direction of approaching wave surge provides lobsters with usable directional information, but the mechanisms by which lobsters use this information need to be defined. In controlled laboratory wavetank experiments, Walton and Herrnkind (1977) have previously shown that blindfolded lobsters are most strongly influenced by water movement at velocities greater than 5 $\mathrm{cm\,s^{-1}}$, but become disoriented in still water. During the present study, local water current velocities were generally lower than this (2–5 $\mathrm{cm\,s^{-1}}$), probably reducing the influence of this potential cue. In addition, current and wave surge have distinct physical characteristics which may provide lobsters with different cues for local environmental features, particularly in the absence of visual cues. Local water currents, for example, tend to be unidirectional and can be highly variable depending on the tidal exchange and the local topography of the area. Alternatively, wave surge is oscillatory, resulting from wind-generated ocean swells passing over the sea bottom (Denny, 1988). Surge could thus provide a steady offshore/onshore directional indicator to lobsters or other reef organisms due to the consistent directional nature of prevailing trade winds (e.g. Herrnkind and McLean, 1971; Walton and Herrnkind, 1977; Lohmann and Lohmann, 1992). Adult lobsters are highly influenced by wave surge and water currents in the field (Herrnkind and McLean, 1971) and these authors have suggested that lobsters use wave surge to guide them during annual offshore migrations as part of a stress response to the first winter storm each year. Lobsters may also move offshore as part of a general reaction to stress, presenting the intriguing possibility that, in the absence of visual cues, spiny lobsters respond to displacement by initially heading into surge, and only later return to the home den (for a review, see Herrnkind, 1980).

An alternative explanation suggests, however, that even when released close to home, displaced blindfolded lobsters are simply lost: they do not immediately know in which direction to walk to find their original den, the reef where a familiar den might be situated or even any temporary nearby shelter. If this is the case, it is possible that a hydrodynamic influence such as the direction of approaching wave surge or local water current, an offshore compass bearing or some other as yet unidentified environmental cue does not point to the location of a specific goal, but rather acts as a unidirectional, navigational cue or 'collimating stimulus' (Pline and Dusenbery, 1987; Dusenbery, 1992). Such a stimulus could serve as a guide in making a straight-line search for a randomly distributed target such as a potential shelter site. If lobsters are trying to locate any object which could give shelter, but have no information regarding the direction of such an object, an efficient course of action would be to walk in a straight line regardless of direction (e.g. Koopman, 1980). This straight-line walk could be guided, for example, by the direction of approaching wave surge, local water currents (Walton and Herrnkind, 1977) or a geomagnetic cue (see Lohmann *et al.* 1995), even though there is no reason to suppose that these cues provide specific information about the location of shelter. Herrnkind and McLean (1971) have shown, for example, that blindfolded lobsters which, upon repeated release consistently demonstrated the strongest directionality, were also not apparently influenced by hydrodynamic cues or any other factors tested. This finding suggests that if lobsters were using these cues for orientation, then they were not using them to signal the direction of a specific goal.

Orientation and release direction

In contrast to the present study, earlier work showed that blindfolded lobsters oriented significantly in the direction imposed on them at release (Herrnkind and McLean, 1971). Several differences in the protocols followed may explain this discrepancy. In earlier studies, lobsters were non-injuriously blinded and released far beyond the home range on a sandy substratum. Here, eye-capped lobsters walked more slowly over eelgrass, but this environment may also have served to distract them from experimentally imposed directional biases. In addition, since the study reported here was conducted relatively close to their dens, our test lobsters were likely to be familiar with the environment of the release sites and potentially less influenced by the release direction imposed upon them than subjects of previous studies. Finally, we tested each lobster only once. Handling stress was further minimized by not bringing lobsters to the surface for transport or eye-capping.

In conclusion, we have shown that the orientation abilities of spiny lobsters are complex and well suited to further study in the field. Our results suggest that spiny lobsters released in the vicinity of their home dens initially orient in a common offshore direction and that their movements are strongly correlated to the direction of approaching wave surge, but not to the direction of their home den or reef. Thus, lobsters may be able to use hydrodynamic cues, a magnetic compass or other as yet unidentified directional cues to orient in and around the complicated environment in which they live. We explore these possibilities further in the accompanying papers (Lohmann, *et al.* 1995; N. D. Pentcheff, G. A. Nevitt, K. J. Lohmann and R. K. Zimmer-Faust, in preparation).

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