

DAILY PATTERNS OF LOCOMOTION EXPRESSED BY AMERICAN LOBSTERS (*HOMARUS AMERICANUS*) IN THEIR NATURAL HABITAT

Walter J. Golet, Darren A. Scopel, Andrew B. Cooper, and Winsor H. Watson III

(WJG, DAS, WHW) Zoology Department & Center for Marine Biology,
(ABC) Department of Natural Resources, University of New Hampshire, Durham, New Hampshire, 03824
(corresponding author (WHW) win@unh.edu)

ABSTRACT

The local movements and activity patterns of American lobsters, *Homarus americanus*, were monitored inside a 50 m by 50 m underwater enclosure (mesocosm) using ultrasonic telemetry. Forty-four lobsters of both sexes, ranging in size from 62 to 93 mm in carapace length, were continuously tracked for 2-10 days in 2002 and 2003. As a population, the movement rate of lobsters depended on time of day, as defined by dawn, day, dusk or night. Lobster movement rates were significantly higher during night and dawn than day and dusk hours. Movement rates did not differ by lobster sex, size or between years of the study. The effect of time of day differed between lobsters, and there was considerable variability in the time of day when individual lobsters were most active. Thirty lobsters moved significantly more during the night, five moved significantly more during the day, and nine did not move significantly more during the day or night. Therefore, while there was a general tendency for lobsters in this study to be more active at night, certain factors in their natural habitat modulated this nocturnal bias, which led to a tremendous amount of variability in their daily patterns of behavior.

INTRODUCTION

Historically, on the basis of field observations by lobstermen and divers, American lobsters (*Homarus americanus*) have been considered to be nocturnal. However, it wasn't until 1969, when Stan Cobb published his PhD thesis, that definitive evidence was put forth indicating that American lobsters in the laboratory are most active at night. Cobb further suggested that lobsters have an endogenous circadian rhythm that is strongly influenced by temperature and ambient light levels. Thirty-seven years later, although a great deal more is known about biological rhythms, both at the molecular and organismal levels, our understanding of lobster activity rhythms in the laboratory and the field has not progressed much further than Stan Cobb's original thesis research.

Although lobster activity rhythms have not been the subject of many studies in the past 35 years, we have made considerable progress towards understanding other aspects of lobster movements. These studies, based primarily on tag/recapture methods, have demonstrated that, although lobsters are capable of long distance migrations (Fogarty et al., 1980; Campbell, 1985; Campbell and Stasko, 1986), the majority of their movements are local. Most tagged lobsters were recovered within 5 km of their release site (Fogarty et al., 1980; Krouse, 1980; Cobb and Wang, 1985; Watson et al., 1999). This tendency of lobsters to carry out both long- and short-distance movements is likely due in part to the activity state of the animal at the time of the study. In several long-term (> 1 year) studies on the territorial behavior of the American lobster, individuals were identified as either residents or transients, based on their observed behavior throughout the study (Stewart, 1972; Ennis, 1984a; Karnofsky et al., 1989). Residents were observed on more than one occasion during the study, while transients were seen only once. Telemetry studies suggest that lobsters have three distinct patterns of movement; local

meandering, medium distance locomotion and rapid excursions (Watson et al., 1999). Similar patterns of movement have also been identified in the spiny lobster *Panulirus cygnus* (Jernakoff, 1987). While these overall patterns of lobster movement are currently widely accepted, little is known about small-scale, local movements that lobsters express when they are residents in a given habitat for more than a few days. In particular, we have a very poor understanding of the biological rhythms manifested by American lobsters in their natural habitat.

Because of their level of control, laboratory studies have yielded the best information about lobster activity rhythms. In the laboratory, lobster activity begins to increase at sunset, peaks within the next few hours and steadily declines as morning approaches (Cobb, 1969; Reynolds and Casterlin, 1979; Lawton, 1987; Wahle, 1992; Jury, 1999; O'Grady et al., 2001; Jury et al., 2005; Mehrtens et al., 2005). Furthermore, one recent study has confirmed Cobb's assertion that lobsters possess an endogenous circadian clock that drives this pattern of nocturnal behavior (Jury et al., 2005). However, while laboratory studies are useful for identifying the tendency of a species to be active at a certain time of the day or night, or for determining if such a pattern is driven by an endogenous clock, the true pattern of activity expressed by an animal in its natural habitat is often influenced by additional factors.

Most observations of American lobsters in the field have revealed patterns of activity that are similar to those expressed in the laboratory. Typically, lobsters retreat to shelters during the day, emerge from their burrows in the evening, have their peak of activity in the first few hours following sunset and gradually decrease overall activity as sunrise approaches (Cooper and Uzman, 1980; Ennis, 1984b; Karnofsky et al., 1989). However, in some instances, ovigerous females (Jarvis, 1989), lobsters in deep turbid waters (Stewart, 1972), those captured during daytime trap

saturation studies (Jury et al., 2001) and lobsters inhabiting rivers (Maynard and Conan, 1984) have all expressed elevated diurnal activity. Interestingly, differences in the expression of activity patterns between laboratory and field studies in other crustaceans have also been documented (Chatteron and Williams, 1994), and suggest cues not replicated in the laboratory are influencing lobster movements in the field. Despite the likelihood that the activity expressed in the field would differ from patterns documented in the laboratory, our working hypothesis was that lobsters would be more active during the night than during the day.

The majority of field studies documenting lobster activity have used either diver observation (Ennis, 1984a, b; Karnofsky et al., 1989) or manual acoustic tracking (Maynard and Conan, 1984; Jarvis, 1989; Watson et al., 1999). Each of these methods can present problems when used to evaluate the presence or absence of activity patterns. Diver observation tends to be intermittent and limited to certain times of the year, sea conditions and to a lesser extent, time of day. As a result, in contrast to more rigorous laboratory studies, a biological rhythm must be determined based on a limited amount of discontinuous information. This is also true for manual acoustic telemetry studies, which yield a limited number of positional fixes, with a spatial resolution of ~20-50 m, depending on local conditions and the system being used (Jarvis, 1989; Watson et al., 1999). Therefore, because it is so difficult to obtain accurate and continuous locomotion data from most marine species in the field, our understanding of the activity rhythms expressed by these animals in their natural habitat is quite limited.

Over the last decade, advances in ultrasonic telemetry technologies have made it possible to monitor the movements and activity patterns of marine organisms in the field with greater spatial and temporal resolution. In particular, automated tracking systems, based on an array of buoys, are capable of triangulating positions with a resolution of 1-2 meters in good sea conditions (VRAP model, VEMCO Ltd., Halifax Canada). The other major advantage of an automated fixed array telemetry system is that positional fixes can be obtained every 1-5 min, so that all changes in activity, during either the day or night, are always recorded. However, even with the advent of these fully automated, high-resolution ultrasonic tracking systems very few studies on the fine-scale movements of lobsters in their natural habitat have been completed using this technology (Factor, 1995). To date, scientists have not succeeded in tracking multiple American lobsters, of both sexes and of varying sizes, for extended periods of time using this technology because: 1) lobsters tend to move outside the range of the tracking system, resulting in the loss of data and expensive transmitters (van der Meeren, 1997); 2) in certain rocky habitats positional fixes are difficult to obtain and thus data collection becomes very intermittent (Smith, G. W. et al., 1998); and 3) there is a limit to the number of animals that can be tracked at any given time due to the dispersal of multiple tagged individuals (Watson, personal observation). In an effort to reduce the likelihood of these problems occurring, and to maximize the accuracy of the VEMCO

VRAP telemetry system that was used in this study, we conducted this investigation within a large underwater enclosure (mesocosm) constructed in habitat that was both suitable for lobsters and conducive to ultrasonic tracking.

While the lobsters we studied were unable to walk long distances in any given direction, the use of a mesocosm allowed us to overcome all of the aforementioned problems and obtain very accurate and continuous data concerning the activity rhythms of a large number of American lobsters in their natural habitat. While the results obtained further support Cobb's original conclusion that lobsters tend to be nocturnal, we were surprised by the high degree of variability in the patterns of locomotion expressed by individual lobsters. In particular, all the lobsters in the study displayed a large amount of activity during at least one of the days they were tracked. It was also surprising to find that lobsters of all sizes and sexes expressed the same patterns of locomotion and moved similar distances. Finally, this study clearly demonstrates the power of ultrasonic telemetry as a tool for investigating the small-scale behavior of lobsters.

MATERIALS AND METHODS

Study Site

This study was conducted in a cove just offshore of New Castle Island, New Hampshire USA (Fig. 1), from June to October, in 2002 and 2003. The average depth in this area is 7-8 meters and the bottom inside the mesocosm consisted of two distinct habitat types: sand and fine sediment (75%) and eelgrass (25%, mostly along the north side closest to shore). The bottom temperature ranged from 8-19°C (monitored with light/temp HOBO data logger) during the course of the study and, as expected, changed with each tidal cycle, as well as with the season. Current speed ranged from 0.03 to 28.9 cm/sec (current was monitored with a Falmouth Scientific Inc. Model 2ACM-CBP-S current meter located a meter above the bottom in the center of the enclosure).

Mesocosm

In the spring of 2002, a large (~ 50 m × 50 m) underwater enclosure (mesocosm) was constructed at the study site. This served to: 1) retain lobsters within the range of the tracking system; 2) allow recovery of tags after tracking individual lobsters for a week; 3) make it easier to relocate lobsters and confirm tags were still attached and had not been lost due to molting; 4) improve analysis of how different lobsters utilized the same habitat; 5) increase the probability of observing tagged lobsters with underwater video stations; 6) track lobsters within an area containing no lobster traps (lobstermen were asked not to set traps inside the mesocosm); 7) maximize the number of times all three buoys simultaneously detected the tag on a lobster so that a position could be calculated; and 8) provide the highest resolution possible, since the enclosure was centered inside the buoy triangle where the accuracy of the system is greatest.

The mesocosm was constructed from standard lobster trap material (12 gauge vinyl-coated wire, 4.0 by 4.0 cm mesh). The walls of the enclosure were 50 cm high with a 32 cm lip (25 cm bent in at a 45° angle, the remaining 7 cm bent down parallel with the wall) to prevent lobsters from crawling over the fence (Fig. 1). Lobsters outside the enclosure were capable of climbing into the mesocosm and were periodically removed to keep densities similar inside and outside of the mesocosm. Seven cm spikes at the bottom were pushed into the sediment to prevent animals from burrowing under the fence. One meter-long pieces of rebar were pounded into the bottom every 3 m and the fence was secured to the rebar stakes using plastic cable ties. Three sides of the mesocosm measured 50 m long and the fourth side was 75 m, giving the enclosure a total area of approximately 3125 m². In addition, 8 PVC "shelters" were secured to the bottom, four in the middle of the enclosure and one midway down each of the four walls.

On six occasions dive surveys were conducted to estimate the number and density of lobsters within the mesocosm. Divers covered 30-40% of the mesocosm during each survey, counting all lobsters observed. From these data the mean density of lobsters was determined (0.04 ± 0.02 lobsters/m², mean \pm SD, range 0.03-0.09) and this value was used to estimate the total

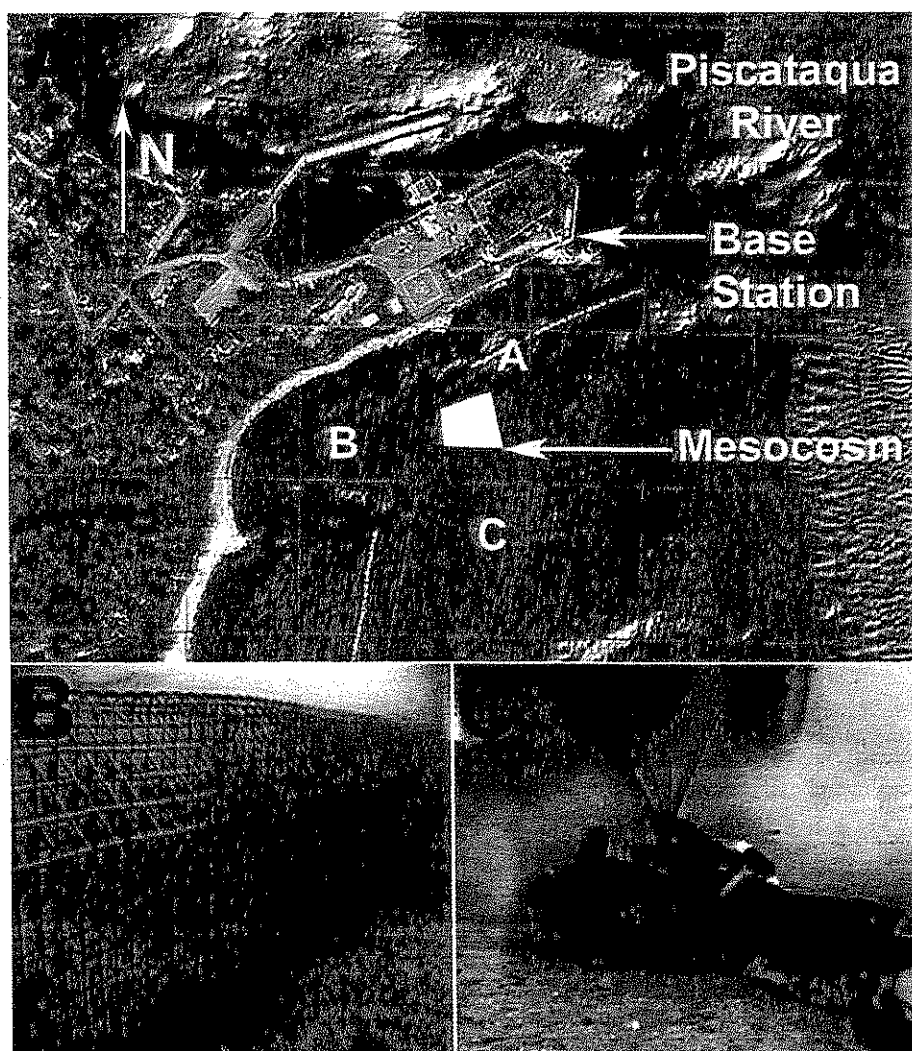


Fig. 1. Study site and method of tagging. A, Outline of the mesocosm, located in a small cove at the mouth of the Piscataqua River, off New Castle Island, NH. A satellite image superimposed with both multi-beam and side-sweep sonar images shows the contour of the river bottom. Each side of the mesocosm is ~50 m long. VEMCO buoy locations are marked with letters. The base station was located approximately 300 m from the site inside either the National Marine Fisheries Service building or the University of New Hampshire Coastal Marine Laboratory. B, Section of fence secured to the bottom at the study site showing the lip design used to prevent lobsters from escaping. C, Lobster being released by a diver after securing a transmitter to the dorsal carapace using a cable tie.

number of lobsters within the enclosure (146 ± 83 , range 100–293). By comparison, in a separate study, we used dive surveys to determine the density of lobsters in both sand (range of 0.001 to 0.06 lobsters/m²) and rocky habitats (0.01–0.06 lobsters/m²) along the same NH coast (Jury et al., 2001). By comparing the results of these surveys, it appears that the density of lobsters within the mesocosm was very similar to adjacent areas of the NH coastline.

Video System

Underwater time-lapse video observations were carried out using a custom system designed and built for this purpose. A waterproof black and white, low light, video camera was placed on a tripod facing one of the PVC shelters in the middle of the mesocosm. This camera was attached to a surface buoy via waterproof cable that both supplied 12-volt DC power to the camera and transmitted a video signal to the surface. The surface buoy contained batteries, a timer and a video transmitter so that video signals could be continuously transmitted to a video receiver located in a building on shore. The video obtained was recorded on VHS tape with a Sony time-lapse recorder. The timer in the buoy limited recording times to the hours between sunrise and sunset, in order to save power. This video system was not used throughout the entire study. Rather, on seven days during the

summers of 2002 and 2003 the system was deployed so that the behavior of lobsters in the vicinity of a shelter could be observed. Due to technical problems, weather, strong currents and other factors that influenced the clarity of the videos obtained, only data from 8 videotapes, representing a total of 56 hours of observation during 7 days, were analyzed to obtain the values presented in this paper.

Tracking System

A commercially available ultrasonic tracking system (VRAP, VEMCO Ltd., Halifax Canada), consisting of a three-buoy array and base station, was deployed at the study site. Two buoys were moored along the north side of the enclosure (shore side) and one just off the south wall, in a roughly equilateral triangle (side 1:150 m long, side 2:151 m, side 3:140 m) (Fig. 1). The buoys communicated to a shore station that was located in a building approximately 300 m from the study site. The system plotted real-time positions of tagged lobsters based upon signal arrival times received by each buoy (for a complete description of the tracking system see Klimley et al., 2001). The buoys listened for each transmitter for 25 seconds and then used the best 70 percent of the signals received to plot a mean X,Y position. A total of 2–4 lobsters were tracked at any given time, with positions calculated every 2–5 min for each animal.

Crystal controlled transmitters (model V8SC-2L, 28 mm \times 9 mm, 3 g in water) that produced an ultrasonic pulse every 2 sec, were used to track lobsters. Each transmitter was set to transmit at a different, stable, frequency (63–84 kHz) so each lobster could be identified. Tags were glued inside a small section of tubing, which was then secured to a cable tie, so that tags could be affixed to lobsters by divers in situ. While control studies were not carried out to determine if transmitters influenced the activity of lobsters, it appears unlikely for two reasons: 1) previous laboratory studies by Atkinson et al. (2005) have demonstrated that ultrasonic transmitters have no effect on spiny lobster locomotion; and 2) the lobsters we tracked inside the mesocosm moved at least as far, and with the same general activity patterns, as lobsters in the laboratory without tags (O'Grady et al., 2001; Jury et al., 2005).

A single reference transmitter was anchored in the center of the enclosure (model V16, 90 mm \times 16 mm). This transmitter was coded at the same pulse interval, but with a separate frequency, and its position was recorded every ten minutes for the duration of the study. It was used, in part, to compensate for buoy movements that caused position errors. Under optimal conditions inside the buoy array it has been estimated by VEMCO Ltd that an accuracy of one meter can be obtained. At this site, the buoys shifted independently due to winds and currents, thus increasing the estimated resolution to one to three meters. However, because we were able to subtract the hourly "movements" of the stationary reference pinger from the hourly movements of lobsters in the same area, these small tracking errors did not significantly influence the types of activity calculations presented in this paper.

Tracking Protocol

Forty-four lobsters of both sexes (20 females, 24 males) with carapace lengths ranging from 62–93 mm, were tracked during the study period. Typically, during a given "run" a group of four lobsters were tracked for five days. At the beginning of each run divers attached ultrasonic transmitters to two male and two female lobsters that resided within the enclosure. The molt stage of each lobster was visually assessed prior to tagging and efforts were made to avoid using pre- and post-molt lobsters. It was not possible to determine how long lobsters had been inside the enclosure before they were tagged because new lobsters were continually entering the mesocosm. Transmitters were secured onto the dorsal carapace of each lobster by connecting the cable tie between the second and third pair of walking legs (Fig. 1). The tagging process took ~2–3 minutes and lobsters were immediately released exactly where they were captured. All lobsters removed from shelters for tagging were returned to the same shelter. This method of rapidly tagging lobsters in situ, without bringing them to the surface, was used because in a previous study it reduced the distance traveled during the first night post-tagging (Lund et al., 1973). No ovigerous lobsters were used in this study. Upon completion of a "run" divers recovered the four lobsters, removed the transmitters and released the lobsters outside of the mesocosm away from the study site.

Data Analyses

The VEMCO software generates files which include the calculated position of each pinger along with concurrent data on ambient noise level, system gain, number of pings received by each buoy and the standard deviation of the arrival times, of every ping, to each buoy. Several factors can affect the accuracy of arrival time calculations, which in turn affects position accuracy. For example, thermoclines, boat traffic and general signal attenuation can all produce inaccurate position fixes. We developed a data filtering protocol to eliminate erroneous points due to some typical errors in signal positioning. This protocol was applied to positions from a stationary reference pinger to determine the optimal filtering level for each parameter. It was then applied to the 44 lobsters used in this study. First, the system averaged the best 70%, out of a maximum of 20 "hits" received during a sampling period, which would often yield 13–16 points per sampling period to average. When this figure dropped to below 7 hits per sampling period, the resulting value was questionable and it was filtered out. Second, when noise levels in the area were high, primarily due to waves and boat traffic, poor resolution was often the result, so points obtained during noisy periods (as indicated by the software, high noise and gain values) were eliminated. Third, when pings were very faint, possibly due to the location of the lobster relative to the buoys, or with respect to an obstruction, the system needed to increase the gain in order to hear the transmitters and this often yielded unreliable points; so these points were not used for subsequent calculations. Finally, when the software averaged the position of the lobster, based on 8–16 fixes, it also calculated the standard deviation of the arrival

time of the pings. Positions with standard deviations larger than 250 ms were likely to produce inaccurate positions. As a result if the SD was >250 , indicating a wide scattering of the points used to calculate the final position, this point was not used for further analyses. This filtering method, although highly conservative, was helpful in reducing scatter of the data, especially when animals were stationary or hidden in shelters (Fig. 2). Most importantly, this filtering technique served to remove false distance traveled data that resulted from spurious points. For example, if the data for the lobster in Fig. 2 were not filtered, 3630 meters would have been added to the overall distance traveled during the entire run, significantly overestimating the distance the lobster actually moved during that time period. On average the system was able to obtain enough information to calculate a lobster's position 600 times during a given 24 h period. After this four-step filter was applied to these data about 54 percent of the original points remained. This resulted in an average of 312 positional fixes for each lobster, per day, or about 13 per hour.

To assess the ability of the VRAP system to calculate accurate positions either inside the mesocosm/array or outside of it, we performed two different tests. First, we determined the number of accurate positional fixes obtained from 6 lobsters that we successfully tracked for at least 24 hours after they escaped from the enclosure. We averaged these data and compared them to similar data obtained from 8 lobsters that were tracked during the same 24 h time period inside the mesocosm. The accuracy or resolution test involved placing a stationary reference pinger outside the mesocosm and then comparing the "home range" or size of the circle of points obtained during a 24 h period, with data collected from a reference pinger inside the enclosure on the same day. The area of a given distribution of points was calculated using the Animal Movement Analysis Extension (AMAE) (Hooze et al., 2001) for ArcView 3.3 (ESRI, Redlands, CA, USA). This comparison was performed on 5 occasions in 2005.

Many of the statistical tests below were carried out using filtered data. In some instances, while calculating the distance traveled during each hour of the day, the distance moved by the stationary reference transmitter was subtracted from the distance moved by each lobster. As the buoys in the array moved due to currents, wind and tides, false distance was added to transmitter positions (see Fig. 2). By subtracting the distance moved by a stationary transmitter during a given hour of data collection, from the distance moved by each lobster tracked during that same hour, it was possible to partially compensate for these buoy movements.

Before data were analyzed, the first twelve hours were removed from each run. Although no significant differences in locomotion were found in the first 12 h vs. the remainder of the recording period for these lobsters, post-handling stress has been known to increase locomotor activity in some crabs (Skajaa et al., 1998) and lobsters (Jernakoff, 1987; Jernakoff et al., 1987; Jarvis, 1989). Tagging procedures in these previous studies involved bringing the animal to the surface and attaching tags. Divers attached the transmitters in this study in situ and lobsters were released within minutes of capture, which appears to have reduced post-handling hyperactivity.

In order to test whether lobsters are more active during certain times of the day the distance moved during transition from one point to another was placed into one of four categories; day, night, dawn, dusk. Daytime was that time from one hour after sunrise until one hour before sunset. Dawn and dusk periods contained all movement data that occurred one hour before and after sunrise and sunset, respectively. Finally, night categories contained movement data obtained from one hour after sunset to one hour before sunrise.

Due to the type of data and the manner in which it was collected, a standard analysis of variance was not appropriate. Unequal numbers of observations between lobsters and the fact that those observations were not independent of each other, violate two assumptions of an ANOVA. Furthermore, averaging the dawn, day, dusk, and night movement rates for each lobster, and thus having 44 estimates of movement rates for dawn, day, dusk, and night is also inappropriate because it ignores the variability inherent in each lobster. For these reasons, we used a generalized linear mixed-effects (GLME) model with Poisson error and log link to determine if lobsters moved significantly more during the four aforementioned time periods (Breslow and Clayton, 1993). These models are similar to linear regression, but directly account for the repeated-measures nature of the data and allow for individual lobsters to differ from one another. GLME models contain two types of parameters: fixed-effects and random-effects. The fixed-effects describe the general trends of the population, e.g., whether lobsters, on average, move more at night than during the day, whereas the random-effects describe how different the individuals are from one another, e.g., Lobster #12 moves \times m/h more at night than does the average lobster.

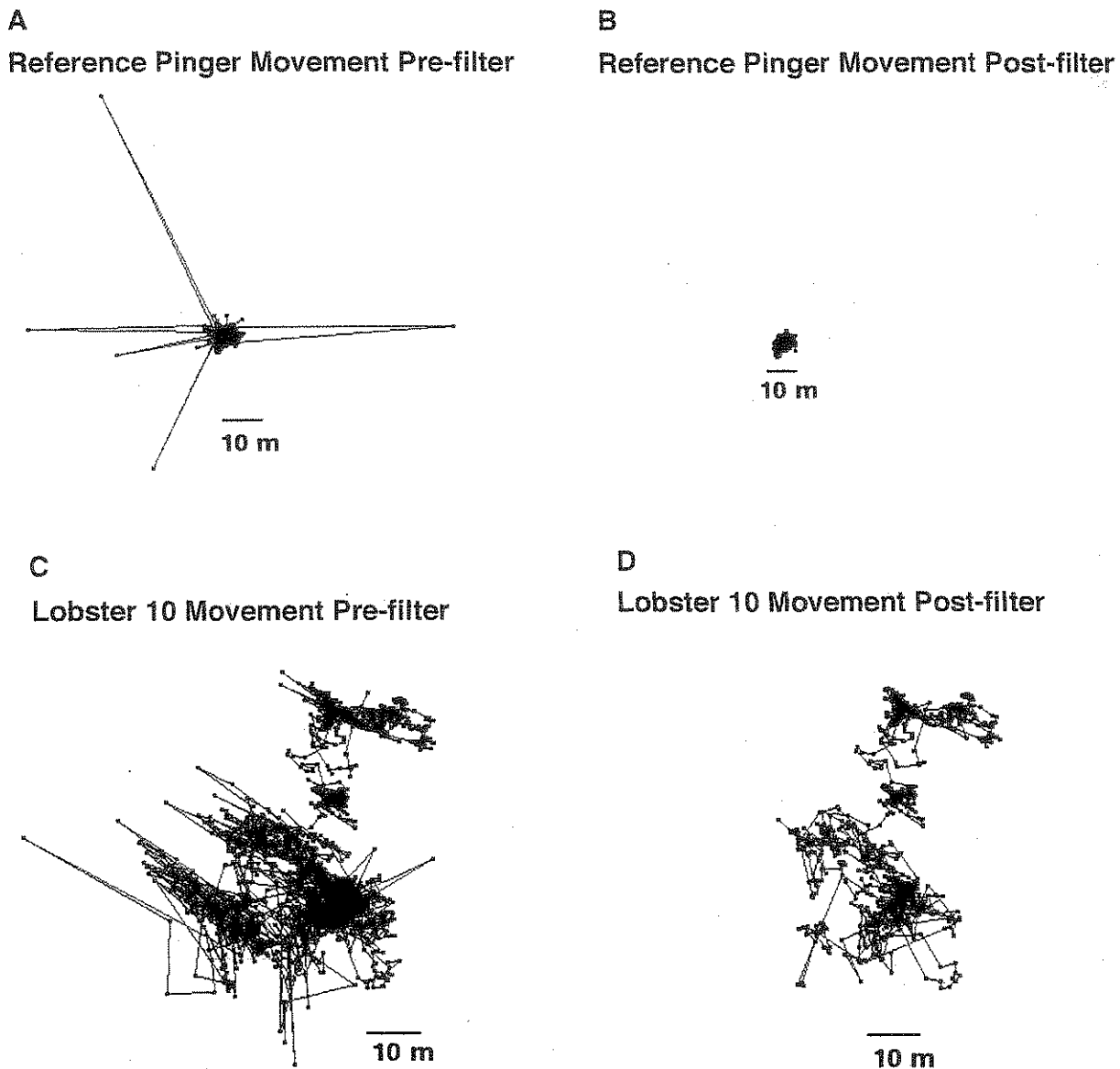


Fig. 2. Lobster and reference transmitter plots demonstrating the effects of filtering. A, Raw data from the stationary reference transmitter prior to any filtering. Notice several points (flyers) that are clearly the result of positioning errors. B, Reference transmitter movements after running the data through the four part filter described in the methods. Erroneous points were removed and the sphere of points was tightened. Even with the filter the stationary transmitter still appears to move a bit due to tidal and wave-driven movements of the individual buoys in the array. C, Movement of a 62 mm CL female lobster over the course of five days prior to filtering. The data appear scattered and several points are well away from the main body of points during a period when the lobster was stationary in a shelter as confirmed by diver observation. D, Track of the same lobster for the same time period after filtering. Notice the track has been condensed and several of the points extending well away from the main plot have been removed.

We used S-PLUS 6.2 for Windows (Insightful Corp., Seattle, Washington, USA, 2003) and the GLME extension from the S+ Correlated Data library (version 1.0, Release 1) within S-PLUS 6.2. The GLME extension implements the methods in Breslow and Clayton (1993). The significance of each fixed-effect was determined using marginal *F*-tests (Pinheiro and Bates, 2000) with an alpha-level of 0.05 for main effects and 0.10 for interaction effects (Sokal and Rohlf, 1981). Movement rates were analyzed at the scale of m/min because that was the scale at which data was collected; however, to be consistent with the way in which this information is typically reported in the crustacean biology literature, all results have been converted to m/h.

Even though the GLME can estimate general trends for the population and describe how individuals differ from one another, GLMEs cannot be used to statistically test whether an individual lobster, e.g., Lobster #12, moves more during the day than during the night. To determine whether each individual lobster was significantly more or less active during the day

versus the night, we used extended generalized linear regression models (Breslow and Clayton, 1993; Wolfinger and O'Connell, 1993). These are similar to linear regression models but are for repeated-measures data. The lobster identification number was treated as a fixed effect and included as a 44-level factor as a main effect and interacted with time of day (as defined by day versus night, dawn and dusk observations were omitted from the model) without a main effect for time of day. This allowed us to directly test for the significance of time of day for each lobster separately, with significance at the 0.05 level. This approach, however, could not be used to describe population-level patterns because of the way each lobster is treated in the model.

All lobsters occasionally encountered the wall of the mesocosm at some point during the course of the study. To examine the potential impact of these wall interactions on the daily activity rhythms expressed by lobsters, we first categorized each day of their activity according to the degree to which they interacted with the mesocosm wall. We used lobster days as the

time period for this analysis, because no lobster exhibited the same type of behavior for the entire study. During Type 1 movement days, a lobster never interacted with the fence, during Type 2 days they occasionally touched the wall, on Type 3 days lobsters came into contact with the wall about 25% of the time and on Type 4 days a given lobster spent more than 50% of the day near the fence. We then ran the final GLME model on each type of lobster movement day separately and examined the coefficients and significance of the fixed effects to determine if the types of day (degree of interaction with the fence) influenced the daily pattern of lobster activity.

RESULTS

Experimental Procedure and System Performance

Out of the 63 lobsters originally tagged, 44 yielded sufficient data for analysis of movement patterns. The remainder either: 1) escaped the enclosure before we had obtained at least 2 days of continuous tracking data; 2) were equipped with transmitters that did not work properly; or 3) were fitted with transmitters that fell off and were found by divers. The remaining 44 lobsters were tracked over a total time period of 210 days. During this 210-day period, 119 days were spent actively tracking lobsters; the interim time was needed for charging the buoys and routine maintenance. An average of 1095 positional fixes/lobster were recorded and a total of two to nine days of movement data were obtained from each lobster, excluding the first 12 hours of data gathered immediately after they were tagged.

The VRAP system was much better at detecting ultrasonic pulses emitted by transmitters on lobsters inside, than outside, of the mesocosm. We confirmed this by comparing data from 6 lobsters that escaped from the mesocosm during the study, with 8 lobsters that were tracked simultaneously inside the mesocosm. When lobsters were inside the mesocosm we obtained an average of 383.4 ± 97.8 (average \pm SD, range 182–480, $n = 8$) useful positional fixes every 24 h, after filtering the data. In contrast, when they were outside the mesocosm, yet still within the detection range of the array, we were only able to collect enough data to yield 42.1 ± 28.0 fixes per day (range = 2–97, $n = 6$). The accuracy of the system also deteriorated when lobsters ventured outside of the middle of the buoy array. We used a home range analysis program to compare the area encompassed by the group of positional fixes simultaneously collected from 5 reference pingers placed inside the mesocosm vs. 5 reference pingers outside the mesocosm. In 24 h, the mean diameter of the "circle" of points was 8.7 ± 1.6 meters (mean \pm SD, range = 6.2–10.4) inside the mesocosm vs. 19.9 ± 1.2 meters (range = 18–21.5) outside. Moreover, the distribution of points outside the mesocosm was often in the shape of an oval and the calculations above are based on the short diameter of the oval, thus yielding a conservative estimate of the ability of the system to track animals outside of the middle of the buoy array.

Lobster Activity Patterns

The movement rate of the 44 lobsters used in this study depended on time of day ($F_{3,58359} = 11.86$, $P < 0.0001$). During the night and dawn lobsters moved more per minute than during the day ($P < 0.0001$ and $P < 0.0001$, respectively) (Fig. 3). Movement rates during dusk, however, were not different from those during the day

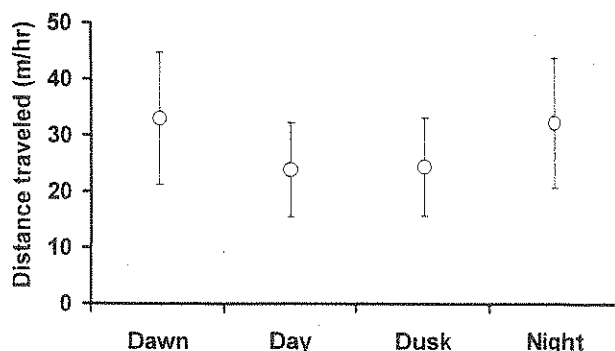


Fig. 3. The GLME model movement rates (mean and SE) for all lobsters during dawn, day, dusk and night. Rate of travel was significantly higher at night and dawn than during the day or dusk.

($P = 0.62$). As a group, the hour of the day during which lobsters traveled the furthest was 4:00 am. (Fig. 4).

Movement rates did not differ by lobster sex ($F_{1,42} = 0.17$, $P = 0.68$), lobster size ($F_{1,42} = 0.07$, $P = 0.79$) or the year of the study ($F_{1,42} = 0.24$, $P = 0.63$). The mean walking rate for lobsters in this study was 0.71 m/min. However, lobsters often expressed bursts of locomotion during a given hour that, on occasion, reached levels as high as 2.77 m/min (this would translate into 166 m/h or 3.98 km/day).

Individual lobsters expressed different patterns of activity. If a lobster moved at about the same rate during a specific time period (day, night, dawn, dusk) day after day, then that lobster would be described as having relatively low movement rate variability, regardless of how much the lobster actually moved. In contrast, if during a specific time period (day, night, dawn, dusk) a lobster moved a lot on some days and very little on other days, then that lobster would be described as having a relatively high movement rate variability. GLME models allow us to directly examine movement rate variability. Movement rate variability differed by lobster (Chi-square₄₃ = 18,707, $P < 0.0001$); some were highly variable and some were not, and lobsters that moved more had higher movement rate variability than those that moved less (Chi-square₁ = 33,749, $P < 0.0001$). Out of the 44 lobsters investigated with the GLME, based on the fixed and random effects, 32 lobsters (73%) had predicted movement rates that were higher during the night than during the day, and 12 (27%) had higher predicted movement rates during the day than at night. However, as previously stated, GLMEs do not allow us to test whether these predicted rates are significantly different from one another for specific lobsters.

Based on the extended generalized linear regression model treating lobster as a fixed effect in order to test the significance of time of day for specific lobsters, 30 lobsters (68%) had expected movement rates significantly higher during the night than during the day, 5 lobsters (11%) moved significantly more during the day than during the night, and 9 lobsters (20%) did not move significantly more during the day or night (Fig. 5). However, given the variability in movement rates mentioned in the GLME model, the fact that a lobster moves more during the night than during the day, on average, does not imply that the lobster always moves more during the night than during the

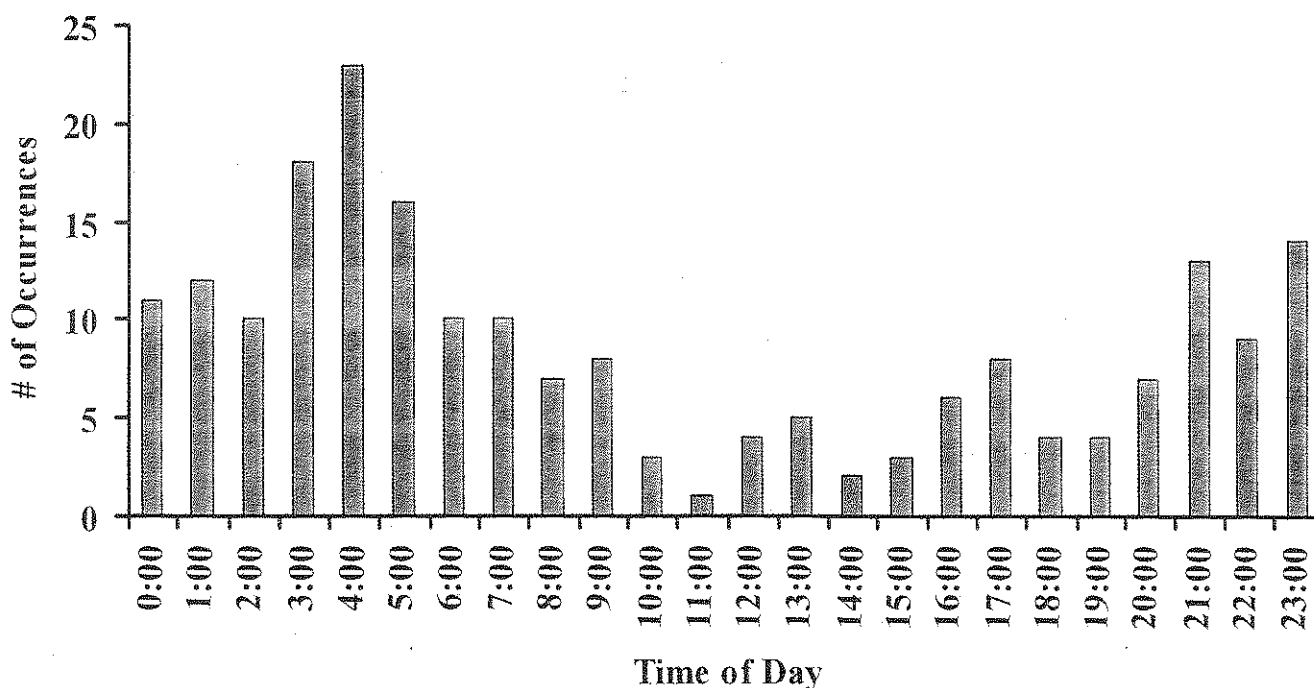


Fig. 4. A frequency distribution showing the time of day when lobsters were most active. The hour in which a given lobster was most active was recorded for each day it was tracked. Then the number of times that a given hour was the maximum was determined for all lobsters over the two-year tracking period and these were summed and plotted vs. the time of day.

day. Some night-moving lobsters moved a great deal during some days, and some day-moving lobsters moved a great deal during some nights (Fig. 6A, B).

During any given day many lobsters spent a portion of the time near the border of the enclosure. In order to determine if interactions of lobsters with the mesocosm wall influenced their natural activity rhythms, we compared the activity patterns of lobsters that interacted with the wall in differing amounts. When applying the GLME to the subset of types

of movement days (e.g., 1,2,3,4), time of day (as defined by day, night, dawn, dusk) was significant in all cases ($P < 0.0001$, $P = 0.026$, $P = 0.0006$, and $P < 0.0001$ for types 1, 2, 3, and 4, respectively). This indicated that the mesocosm did not significantly influence the time of day during which lobsters were most active (Table 1).

Time-lapse videos of lobsters in the vicinity of a shelter were obtained on 7 separate days for a total of 56 hours. During this 56 h observation period lobsters departed from the shelter being observed ~once/hour (48 times, 0.86 times/h). In 58% of the cases lobsters spontaneously left the shelter, while on 20 occasions (42%) they were evicted by another lobster. Of the 58 encounters that took place between a lobster inside the shelter and one outside, 34% resulted in evictions and during the remainder of the encounters (66%) lobsters successfully defended the shelter. On no occasion did a lobster defending a shelter come all the way out of the shelter. Thus, according to these observations, while lobsters often defended their shelter, both evictions and spontaneous departures were common. As a result, the chance of a given lobster occupying the same shelter for an entire day, without leaving, was very low. However, it was not possible to determine if the same lobster was returning to the same shelter repeatedly.

DISCUSSION

Beginning with the pioneering work of Stan Cobb (1969), a number of studies have linked decreasing light levels to increases in decapod activity in both field and laboratory settings (Copper and Uzmam, 1980; Ennis, 1984b; Jernakoff, 1987; Lawton, 1987; Karnofsky et al., 1989; Wahle, 1992; van der Meeren, 1997; Skajaa et al., 1998; Smith, I. P.

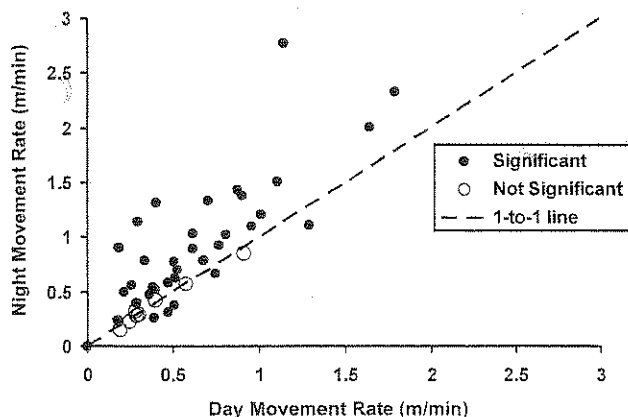


Fig. 5. Movement rates of lobsters during the day and night based on the extended GLME model. Solid black dots above the line represent lobsters with significantly higher movement rates during the night, while solid black dots below the line represent lobsters with significantly higher movement rates during the day (significance derived from the Poisson regression). Open circles represent lobsters for which there was not a significant difference in movement rates between day and night.

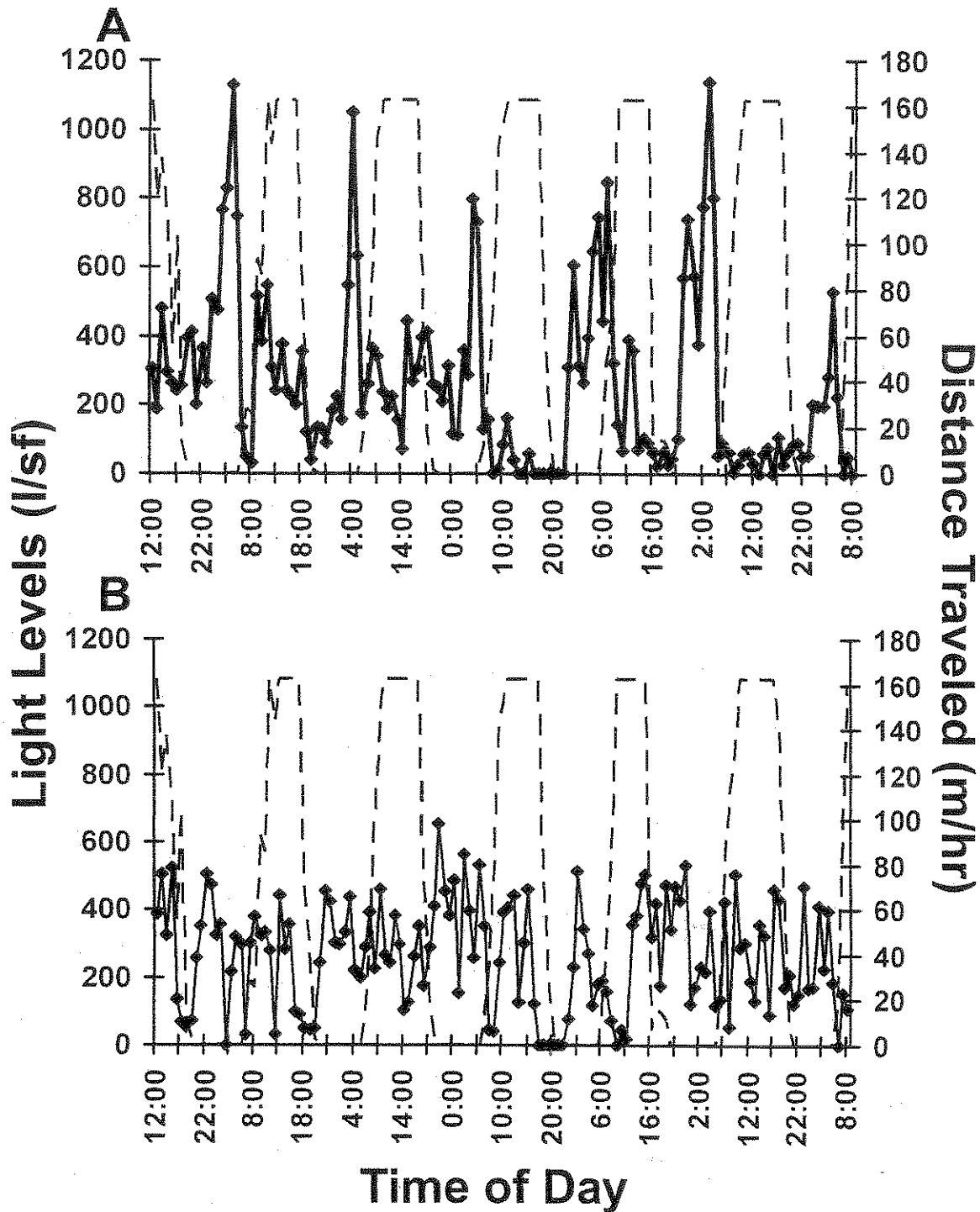


Fig. 6. Distance (diamonds) traveled per hour, during five consecutive days in 2002, by two lobsters (A: 75 mm CL female; B: 78 mm CL female) tracked during the same time period. Also plotted are light levels (dashed line) measured on the bottom of the mesocosm. The HOBO light datalogger saturated during the day and night. Notice that the 75 mm CL female whose activity is plotted in the top graph exhibits a tendency to be most active at night, while the second lobster, whose activity is plotted on the bottom graph, is almost continuously active during both the day and the night.

et al., 1998; Jury, 1999; Smith et al., 1999; O'Grady, 2001). Most recently, Jury et al. (2005) clearly demonstrated that American lobsters have an endogenous rhythm of locomotion that persists for days under conditions of constant darkness, confirming the initial studies by Stan Cobb. In this

study we took advantage of ultrasonic telemetry technology to extend our understanding of lobster biorhythms to animals moving about in their natural habitat.

One of the most striking and surprising findings resulting from this study was that, although there was a tendency

Table 1. Using day as our zero category, and comparing movement rates to the remaining time periods, there was no significant difference in the timing of activity between the different lobster Types (Type 1 = no interactions with fence, Type 2 = occasional encounters with the fence, Type 3 = moderate amounts of time spent near the fence, Type 4 = frequently near the fence, especially one of the corners). The lobsters in the four different categories expressed the same pattern in the timing of their movement, expressed as a percentage of the baseline daytime rate.

Time of day	Type 1	Type 2	Type 3	Type 4
Night	43%	42%	54%	18%
Dawn	35%	33%	40%	31%
Dusk	-19%	-17%	25%	-9%

to be nocturnal, lobsters in their natural habitat expressed patterns of activity that were quite variable. While about 70% of the lobsters tested were most active at night, the rest were either diurnal, or expressed no preference. Furthermore, individual lobsters often switched from being nocturnal one day, to diurnal the next, and some of the highest bouts of activity (distance traveled per hour) were recorded during the day. Often, as indicated in Fig. 6B, activity was spread out throughout the 24 h period with no apparent peak at all. This type of variability has also been observed in the laboratory, with American lobsters, but often to a lesser extent (Lawton, 1987; Jury et al., 2005). In addition, it has previously been reported for other decapods (Jernakoff, 1987; Jernakoff et al., 1987; Barbaresi et al., 1997; Skajaa et al., 1998). In cases where high levels of daytime activity have been observed in American lobsters, such behavior has been attributed to lower light levels due to increased turbidity (Stewart, 1972; Briggs and Mushacke, 1979; Smith et al., 1999). However, at our study site light levels were typically quite high during the day and on those days when light levels were diminished due to clouds and storms daytime activity was not noticeably higher, and there was no correlation between lobster activity and light levels (Golet, 2003). Thus, an alternative mechanism is necessary to explain the occasional bouts of high daytime activity expressed by many of the lobsters in this study, and perhaps in other studies as well.

Even though lobsters in a laboratory setting tend to express an endogenous circadian rhythm (Jury et al., 2005), with most activity occurring at night, our results suggest that the expression of these rhythms in the field must be modified by environmental cues not present in laboratory studies. Strong shelter affinity has been documented for the American lobster (Cobb, 1971; Ennis, 1984a; Karnofsky et al., 1989), and in areas where shelters are relatively scarce competition for these shelters, with resulting evictions, may force lobsters that would otherwise hide during the day to become active in search of suitable shelter. Moreover, it has been demonstrated that the presence of predators, in a laboratory setting, increases the amount of time lobsters reside in a shelter, decreases their foraging activities and influences the extent to which they are active during the day (Lawton, 1987; Wahle, 1992; Spanier et al., 1998). This impact of predators would be expected to play a role in their natural habitat, but this may not have been the case in this study for two reasons. First, many of the lobsters investigated in this study were not small enough to be very sus-

ceptible to the local predators (Wahle and Steneck, 1992; Watson, in preparation). Second, based on the number of lobsters often observed residing in pits in the open sand and our video and SCUBA observations, predation on lobsters was not high in this area. Thus, although shelters were relatively scarce, they were not vital to the survival of the lobsters we investigated. While lobsters often defended their shelters, they were just as likely to leave their shelters either when confronted, or spontaneously. Thus, shelter occupancy was relatively transient and it was rare for a given lobster to occupy the same shelter for extended periods of time (except for mating pairs). In 1987, Lawton observed increased activity of juvenile (< 46 mm CL) lobsters during the daytime in the laboratory when intraspecific interactions were common, and food was scarce, and that appears to hold true for the larger lobsters we studied in the field as well. While our working hypothesis is that these intraspecific interactions are the primary reason lobsters have variable patterns of activity in their natural habitat, other factors, such as the need for more food due to a high metabolism during warmer summer months, preparing for or recovering from molting, and summer mating activities are also likely to influence the extent to which lobsters express consistent biological rhythms in their natural habitat.

In this study, lobsters were most active at 4:00 AM, although this peak in activity is really part of a very broad increase spanning from 10:00 PM at night to 7:00 AM in the morning. Previous reports indicate that the activity of lobsters is minimal during the day, increases as evening approaches and reaches a peak approximately 2-5 h after sunset. Following this period activity levels gradually decline as morning approaches (Cobb, 1969; Ennis, 1984b; Karnofsky et al., 1989; van der Meeren, 1997; Smith, I. P. et al., 1998). In general, given the time of year this study took place, our data illustrate a similar trend. Sunset during the summer occurred between 7:30 and 9 PM and thus peak activity would be expected 2-5 hours after this, or near midnight. Furthermore, despite the fact that animals were often active during the day and the maximum rates of movement we recorded at 4:00 AM, there was a consistent lull in activity in the middle of the day and the greatest movements took place in the middle to late portions of the night.

There are both advantages and disadvantages to using a fixed array ultrasonic telemetry system such as the one employed in this study (VRAP, VEMCO, Inc). The two biggest advantages are: 1) data are collected continuously and automatically; and 2) localizations are very accurate, especially when compared to telemetry approaches that utilize either manual systems or fixed listening stations. To our knowledge this study is one of the largest of its kind in terms of the number of animals investigated and the total amount of data obtained, and it illustrates both of the strengths of fixed array systems quite well (discussed further below). However, fixed array systems also have the following disadvantages that may be responsible for preventing the widespread application of this technology. 1) Freely moving animals usually move out of the range of the array. For example, van der Meeren (1997) encountered this problem and was only able to gather 240 min of data from 4

different lobsters. We are currently expanding our studies to freely moving lobsters and in 2 years we have successfully tracked 6 lobsters continuously for time periods exceeding 3 days (Scopel et al., in preparation). This contrasts with the current investigation, during which we successfully tracked 44 lobsters in 2 years. 2) Positional fixes are considerably less accurate when animals are within range of the system, but not in the middle of the array. While we were able to compensate for the error in this study by subtracting the hourly movements of a stationary reference pinger from those recorded from moving lobsters, this is not always possible. 3) A fixed array system is expensive in contrast to manual systems or listening stations. A complete fixed array system costs more than \$US40,000, while listening stations or manual systems cost less than \$US5000 (the pingers cost about the same for each). 4) Finally, the ability of all the buoys in the array to detect transmitters on lobsters that ventured outside the mesocosm, and hence outside the triangle formed by the buoy array, was poor. As illustrated by the comparison of captive and escaped lobsters, we typically obtained 383 useful points inside the mesocosm in 24 hours. When tracking outside of the mesocosm, even if lobsters were in a habitat that was conducive to ultrasonic tracking, we only obtained 42 points in 24 hours. Nevertheless, despite these disadvantages, if the goal is to understand the small-scale movements of lobsters or other mobile marine organisms during all hours of the day, then fixed array ultrasonic telemetry is currently the best solution, especially if it is possible to study questions that are appropriate for investigation inside a mesocosm.

In order to overcome many of the disadvantages listed above, we tracked lobsters inside a large mesocosm and, overall, the enclosure solved these problems in the following ways. 1) The enclosure kept the animals within the high-resolution zone of the system, as illustrated by the large number of points retained post-filtering. 2) Since the bottom type consisted of eelgrass beds and open sand, acoustic pulses could travel directly to the buoys with no interruption by rocks or other physical barriers. 3) The mesocosm allowed us to track ~4 lobsters at a time, rather than 1-2, greatly increasing the amount of useful data we were able to collect, as stated above. 4) Because our enclosure did not contain any lobster traps it was easier to interpret data. On two occasions lobsters escaped from the enclosure and appeared to have taken up residence in a nearby cove. On one occasion the lobster in question was in a trap, in the other case it was not, and yet according to the telemetry data, the cluster of points generated by both lobsters appeared to be similar. 5) Purely from a financial standpoint, the enclosure made it easy to retrieve transmitters and use them again on other lobsters. When outside the mesocosm, lobsters occasionally moved into deep channels, which made retrieval by SCUBA very difficult and more dangerous. 6) Finally, because all the lobsters were moving about in the same habitat we were more confident when comparing patterns of movement between animals and it was easier to deploy video systems to monitor their activity. In short, while the mesocosm may not be appropriate for certain types of behavioral studies, it does serve as an excellent compromise between a laboratory

setting and a completely natural environment. In particular, given the systems used to study lobster activity rhythms in the laboratory, such as treadmills (O'Grady et al., 2001), running wheels and racetracks (Jury et al., 2005), the mesocosm offers an opportunity to investigate the types of activity patterns expressed by lobsters under much more natural conditions.

We acknowledge that the borders of the mesocosm limited the ability of lobsters to move long distances in a given direction. Because of this concern, we examined the activity patterns of lobsters that interacted with the fence to different degrees. Surprisingly, there was no difference in the daily timing of activity expressed by lobsters designated as Types 1-4, suggesting that the enclosure did not affect their biological rhythms. This is not too surprising given the fact that lobsters express good activity rhythms, with about the same degree of variability in the laboratory while confined to treadmills, racetracks or running wheels. Therefore, we believe that the patterns of behavior reported in this paper are representative of what normally occurs in habitats of this type and, until significantly new approaches are developed, the approach used in this study offers many advantages for long-term studies of lobster behavior.

In conclusion, it appears that, in general, American lobsters are most active at night, as reported by Cobb in 1969. However, variation in this pattern between lobsters, and from day to day for the same lobster, cannot be overlooked. Taken together with recent studies demonstrating the endogenous nature of the lobster circadian rhythm of activity (Jury et al., 2005), it is clear that other variables must be influencing the timing and intensity of lobster locomotion in the field. The methods for tracking lobsters utilized in this study have proven to be highly successful, and should lead to the use of this technology with greater confidence in the future. Further work using this method should focus on isolating and determining how different habitats and environmental cues, along with the behavioral and physiological state of the animal, influence locomotor activity in the field.

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In conclusion, it appears that, in general, American lobsters are most active at night, as reported by Cobb in 1969. However, variation in this pattern between lobsters, and from day to day for the same lobster, cannot be overlooked. Taken together with recent studies demonstrating the endogenous nature of the lobster circadian rhythm of activity (Jury et al., 2005), it is clear that other variables must be influencing the timing and intensity of lobster locomotion in the field. The methods for tracking lobsters utilized in this study have proven to be highly successful, and should lead to the use of this technology with greater confidence in the future. Further work using this method should focus on isolating and determining how different habitats and environmental cues, along with the behavioral and physiological state of the animal, influence locomotor activity in the field.

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