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Daily and circadian rhythms of locomotor activity in the American lobster, *Homarus americanus*

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Abstract

It is widely accepted that American lobsters, *Homarus americanus* (Milne-Edwards), are nocturnally active. However, the degree to which this rhythm is expressed by different individuals and the underlying causes of lobster activity rhythms, are poorly understood. In order to address these issues we recorded daily patterns of lobster locomotion using two novel techniques. In the first, reed switch assemblies were used to monitor the distance traveled by freely moving lobsters (n=43), each fitted with a small magnet, as they walked around a 1 m diameter racetrack. The advantages of this technique included: (1) lobsters were freely moving; (2) the system could be deployed in laboratory tanks or in the field and; (3) actual distances moved were measured, not just relative activity. The second technique involved placing individual lobsters (n=10) into custom-designed running wheels. This allowed for continuous monitoring of locomotor activity for extended durations (>45 days) under normal light/dark (L/D) cycles, as well as in constant darkness (D/D) and constant light (L/L).

Under ambient light conditions lobsters in the racetracks moved an average of 60.1±6.5 m/day in flow-through seawater tanks. Overall, lobsters were significantly more active at night, moving 4.1±0.4 m/h in the dark vs. 1.0±0.2 m/h in the light. However, many of the lobsters moved as much during the day as during the night.

Lobsters in the running wheels moved an average of 36.6±11.7 m/day and 80% expressed clear daily rhythms of activity, with a mean periodicity of 24.0±0.1 h under L/D conditions. Under D/D conditions 90% of the animals expressed free-running circadian rhythms with a mean periodicity of 24.2±0.3 h, indicating that this species possesses endogenous rhythmicity. While the running wheel results show that the nocturnal pattern of locomotor activity for this species is strongly influenced by an endogenous circadian clock, the results from the racetracks show that there is remarkable variability in the extent to which they express this pattern under natural conditions.

Keywords: Activity; Circadian; Homarus; Lobster; Locomotion; Rhythm

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1. Introduction

Many decapod crustaceans synchronize certain behaviors to daily light/dark cycles. Both laboratory and field data suggest that these rhythms are controlled by circadian clocks that are strongly influenced by environmental factors, especially light (Arechiga and Atkinson, 1975; Arechiga et al., 1993; Palmer, 1995; Arechiga and Rodriguez-Sosa, 1997).

Endogenous control of locomotion has been well established for some crustaceans including amphipods (Williams and Palmer, 1988), several species of crab (Taylor and Naylor, 1977; Rebach, 1985, 1987; Chatterton and Williams, 1994; Palmer, 1995; Forward et al., 1997, 2003) and crayfish (Page and Larimer, 1972; Fanjul-Moles and Prieto-Sagredo, 2003). However, the extent to which lobsters, particularly American lobsters, express a circadian rhythm of locomotion that is under endogenous control is not well understood. Nocturnal increases in locomotion and synchronization to the ambient photoperiod have been observed in at least five lobster genera (10 different species) including *Panulirus* (Kanciruk and Herrnkind, 1973; Morgan, 1978; Lipcius and Herrnkind, 1985; Jernakoff, 1987; Nagata and Koike, 1997), *Galathea* (DeGrave and Turner, 1997), *Jasus* (Fielder, 1965; Williams and Dean, 1989), *Nephrops* (Atkinson and Naylor, 1976; Chapman and Howard, 1979; Chapman, 1980; Aguzzi et al., 2003), and *Homarus* (Cobb, 1969; Branford, 1979; Smith et al., 1998, 1999). While *P. japonicus* is likely to have an endogenous clock (Nagata and Koike, 1997) the best evidence for an endogenous circadian clock controlling locomotion in lobsters comes from studies of the New Zealand rock lobster, *Jasus edwardii* (Williams and Dean, 1989) where animals exhibited persistent rhythms under constant environmental conditions. Several studies have suggested that activity of *Homarus americanus* is also based upon a circadian pacemaker with a periodicity of approximately 24 h with peak activity occurring typically around sunset and continuing throughout the night (Cobb, 1969; Stewart, 1972; Krekorian et al., 1974; Zeitlin-Hale and Sastry, 1978; Reynolds and Casterlin, 1979; Ennis, 1984; Lawton, 1987; O'Grady et al., 2001).

As a result of this body of literature, and numerous unpublished observations made using SCUBA and remote video, it is generally accepted that lobsters show nocturnal activity patterns throughout much of their life history (see Factor, 1995). However, recent reports that lobster catch and activity around traps are comparable during the day and the night hours (Jury et al., 2001) as well as SCUBA and video observations of extensive diurnal activity off the coast of NH (unpublished data) prompted us to further explore the locomotor rhythmicity of *H. americanus*. Our first goal was to test the hypothesis that lobsters are nocturnal under ambient light/dark (L/D) conditions by monitoring the locomotor activity of lobsters allowed to freely move in 1 m diameter racetracks.

Several techniques have been used to study patterns of locomotor activity in decapods. The methods traditionally used in the laboratory include monitoring: (1) the mechanical displacement of objects in a tank (Cobb, 1969); (2) the tripping of light beams (Reynolds and Casterlin, 1979); (3) overt behaviors using video observations (Lawton, 1987) and; (4) strain gauges that measure pressure changes as lobsters move in a suspended cage (Koike et al., 1997). A major limitation of these approaches is that they can only monitor relative activity instead of the actual distance traveled by the lobsters. Another drawback is that these studies were not designed to rigorously determine whether or not lobsters possess an endogenous circadian clock. In most of the aforementioned studies circadian rhythmicity was apparent, but uncontrolled exogenous environmental stimuli were also present or the observation periods were too short for appropriate analyses. The second major goal of the present study was to explicitly test if locomotor activity in *H. americanus* is endogenously controlled by continuously monitoring lobster locomotion under L/D conditions, followed by dark/dark (D/D) and light/light (L/L) conditions, for extended periods. Our results indicate that the American lobster possesses an endogenous circadian clock. However, a number of factors appear to be capable of overriding the influence of this clock on overall locomotor activity.

2. Methods

2.1. Animals and environmental conditions

2.1.1. Racetrack experiments

Adult, intermolt lobsters of both sexes (n=43; range 81–95 mm carapace length) were captured in the Great Bay estuary or nearby coastal NH and held for less than 2 weeks communally at the University of New Hampshire's Jackson Estuarine Laboratory, Durham, NH under ambient environmental conditions. They were fed approximately weekly prior to being tested in activity racetracks. In each experimental trial, two lobsters were monitored simultaneously, each in a separate racetrack that was placed within a 2 m diameter flow-through seawater tank located in an outdoor greenhouse. The tank received ambient seawater from the Great Bay estuary and was maintained at a depth of 40 cm. The racetracks were visually shielded from each other within the tank, as well as from movement outside the tank, by sheets of black plastic that were oriented such that ambient light still entered the tank.

Salinity data were recorded with an Endeco CTD meter located near the intake to the laboratory. The water temperature in the experimental tank was continuously recorded with a HOBO Temp datalogger (Onset, Co). Temperatures averaged 16.3±0.6 °C while salinities averaged 26.5±0.3 ppt (but were always >25 ppt). Temperatures in the test tank typically fluctuated less than ±2 °C with each tidal cycle. Light levels in the test tanks were monitored with HOBO Light dataloggers (Onset). In the daytime maximum light levels in the racetracks were generally between 10 and 1000 lumens/m^2, while during the night light levels dropped below the resolution of the logger to <0.75 lumens/m^2. All experiments were conducted from late June to early October, from 1997 to 2000.

2.1.2. Running wheel experiments

Adult lobsters (*n*=10; 82–86 mm carapace length) were maintained in recirculating seawater tanks at approximately 32 ppt at 16±3 °C in a 'light-tight' room at Plymouth State University, Plymouth, NH. Lobsters were not fed for the duration of the individual experiments (45–61 days). Light levels under lighted conditions (i.e., L/D and L/L) were maintained using 2 broad spectrum 20 W fluorescent lights (Simkar, Pittsburg, PA) measured at average values of 25–85 lumens/m^2 at water level (LunaPro light meter, Gossen, Germany). Duration and timing of photoperiod were monitored continuously using a HOBO Light datalogger (Onset). All experiments were conducted during May to July, 2000.

2.2. Experimental procedures

2.2.1. Racetrack experiments

Lobsters with a 1×1″ magnet attached to their dorsal carapace were placed in a 1 m diameter×25 cm wide racetrack made of plastic-coated wire mesh (Fig. 1A). As they walked around the track they passed through two PVC conduits located on opposite sides of the racetrack. These conduits were fitted with reed switches such that when a lobster passed through a conduit it caused a closure of one of the switches, which was then recorded by a datalogger (Hobo Event, Onset). These magnetic switches proved to be much more reliable than optoelectronic detectors due to transient but persistent turbidity in the flow-through tanks that varied the light levels and tended to give false positive trips of detectors reliant upon light. The technique was verified three times by videotaping lobsters moving in the racetrack while simultaneously recording from the reed switches. It was found that all passes were successfully recorded (data not shown). Because of potential handling artifact on activity measurements on the first day of recording, all data presented are from the second 24 h of each trial.

2.2.2. Running wheel experiments

Running wheels for lobsters were constructed from 5 gal plastic buckets (high-density polyethylene) with a 30 cm inner diameter and width of 10 cm (Fig. 1B). They were perforated extensively on all surfaces with >500 holes (6 mm diameter each) to allow water circulation and to provide increased traction. The wheel rotated around a hollow, 1 cm plastic axle fixed to a plastic (PVC) stand. A reed switch located on one leg of each stand detected wheel movement when one of two small magnets, attached 180° from each other on the outer surface of the wheel, passed by it (Fig. 1B). Lobsters were placed individually into the running wheels in a temperature controlled recirculating aquarium. All lobsters were first exposed to a 14:10 L/D cycle for at least 14 days. After exposure to L/D, animals were exposed to D/D for 21–23 days. D/D conditions were initiated by unplugging the light from the timer. D/D conditions were followed by exposure to 10–28 days of L/L.

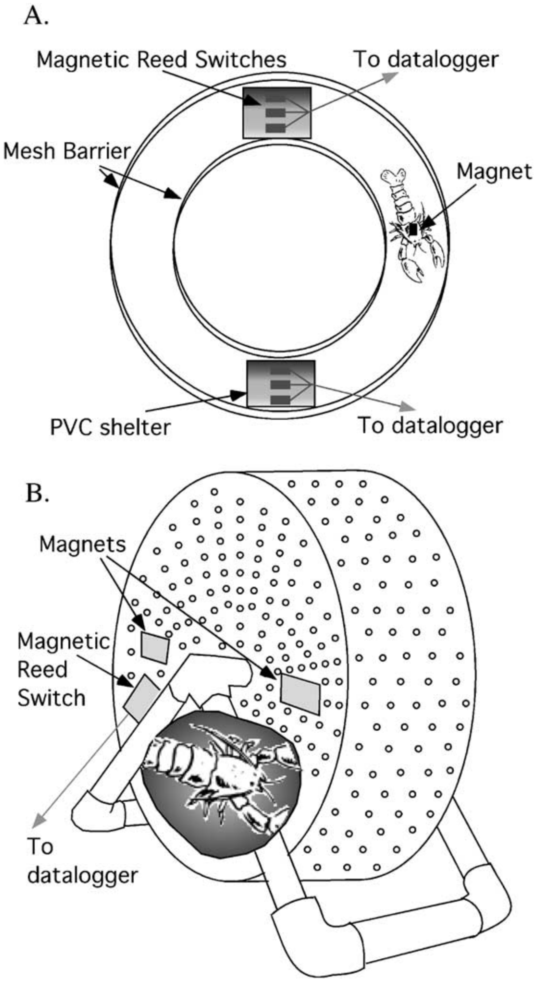

Fig. 1. (A) *Activity racetrack design*. Individual lobsters were placed into a 1 m diameter×25 cm wide racetrack made of plastic-coated wire mesh. Individual tracks were visually shielded and placed in a 2 m diameter flow-through tank. Reed switches were attached to two PVC conduits located on opposite sides of the racetrack. When a lobster passed through a conduit, a small magnet attached to its dorsal carapace caused a switch closure that was recorded at a datalogger. A switch closure in one shelter followed by a subsequent closure in the opposite shelter, and a return to the initial shelter, was considered to be one complete pass around the circumference of the center of the racetrack (2.4 m). (B) *Running wheel design*. Running wheels were made of new 5 gal plastic buckets with a 30 cm inner diameter and a width of 10 cm. They were perforated extensively to allow water circulation and to provide increased traction. The wheel rotated around a 1 cm plastic axle fixed to a plastic stand. A magnetic reed switch located on one leg of each stand detected wheel movement when one of two small magnets attached on the outer surface of the wheel passed by it. Lobsters were individually placed into running wheels in an environmentally controlled aquarium for periods of >45 days.

2.3. Data analysis

2.3.1. Racetrack experiments

The number of times a lobster walked around the racetrack (from one shelter to the other and back again) per hour was counted for the second 24 h of each trial. Distances traveled and rates of movement were determined by multiplying the number of passes by the circumference of the center of the racetrack (2.4 m) to obtain activity in m/day or m/h. Mean activities for all pooled individuals were tested by comparing day vs. night activity (paired *t*-tests). All summary statistics are presented as mean±S.E.M. Significance was assessed at the $p<0.05$ level.

2.3.2. Running wheel experiments

Activity data from the running wheel experiments were collected in 5 min bins using a *Drosophila* Activity Monitoring System (Trikinetics, Waltham, MA). Actograms were plotted using the program Ratman (Ratplot; Klemfuss and Clopton, 1993). The data were analyzed for significant periodicity (Chi-square, $p<0.05$) using a periodogram analysis program (Ratwave; Klemfuss and Clopton, 1993; Sokolove and Bushell, 1978) and visual inspection. In all cases the best Tau, a measure of free running periodicity, was confirmed visually and these values were used in subsequent analyses. Alpha, the length of the main bout of daily activity, was calculated by drawing objective lines of best-fit along the onsets and ends of activity for each animal in both L/D and D/D. Phase angle to the L/D cycle (the time difference between the onset of activity and the onset of darkness) was calculated by measuring the time difference between the drawn lines of best-fit of onset of activity and the onset of darkness, as measured by Hobo light dataloggers. If neither alpha nor phase angle of entrainment were clear in L/D or D/D these animals were excluded from further analysis of alpha ($n=2$) and phase angle ($n=1$). Amount of activity was calculated by multiplying the number of counts per day (where 1 count equaled 0.5 of a wheel rotation) times half of the circumference of the running wheel to obtain activity in m/day. Significance of the differences between means was calculated using either *t*-tests or repeated measures ANOVA (StatView or SuperANOVA, Abacus Concepts, Berkeley, CA, $p<0.05$).

3. Results

3.1. Lobster activity in racetracks

Under ambient L/D conditions, lobsters in the racetrack experiments generally exhibited nocturnal patterns of activity (Fig. 2). As a group, the lobsters used in this study were significantly more active at night than in the day, moving 4.1±0.4 m/h in the dark vs. 1.0±0.2 m/h in the light (paired *t*-test, $p<0.001$, $n=43$). The most common pattern observed was a tendency to be active at night, with sporadic bouts of activity in the day (Fig. 2A). Several lobsters showed extensive daytime activity (e.g., Fig. 2B) and finally, some lobsters exhibited almost no activity (i.e., 16% moved <10 m/day). This suggests that expression of a nocturnal pattern of activity is not robust in this species under ambient L/D conditions in the laboratory. The lobsters that did not express an apparent rhythm ($n=18$) generally moved less per day (27.9±8.7 m/day) when compared to lobsters that did express a rhythm ($n=25$; 83.3±5.9 m/day). The more active lobsters generally showed peak activity near sunset and almost always during the nocturnal period (as reported in previous studies (Cobb, 1969; Cooper and Uzmann, 1980; Lawton and Lavalli, 1995).

It is possible that some of the variability in our results was due to the range of sizes of the lobsters

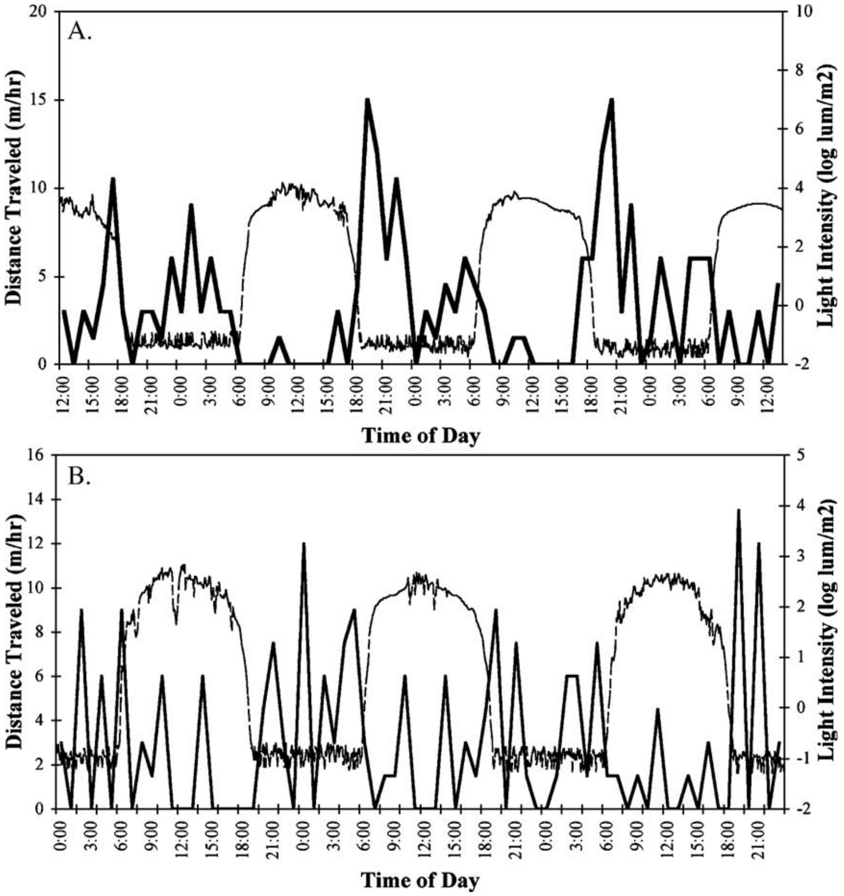

Fig. 2. Typical activity records from lobsters in activity racetracks. Data from one lobster expressing a primarily nocturnal pattern of activity (A) and one lobster that did not express a clear rhythm (B) are shown along with light levels (dotted lines represent light; dark lines represent activity). Both lobsters (A and B) were in tanks receiving ambient environmental cues (e.g., natural illumination). While most lobsters increased their activity at night, the degree to which this was expressed by individuals varied. The majority of lobsters tested showed more activity at night with occasional bouts of activity in the day (similar to A).

used, the range of temperatures they experienced during the months when the studies were conducted, or the mix of sexes in the study group. However, there were no significant differences in distances moved per day between sexes (unpaired t-test, p>0.5); by temperature (r^2=0.082); by month (r^2=0.071); or by size (r^2=0.003). Thus, it is not clear at this time why some lobsters were more nocturnal than others.

3.2. Lobster activity in running wheels

When exposed to a 14:10 L/D photoperiod, lobsters on running wheels became entrained to the light cycle and their activity was primarily confined to the dark portion of the cycle (Fig. 3). The average phase angle of entrainment to L/D was 1.1±0.7 h, which was not statistically distinguishable from zero (one sample t-test, p>0.5). Eight out of ten lobsters showed significantly more activity in the dark than during the light with periodogram analyses yielding an average Tau of 24.0±0.1 h.

When the lobsters were exposed to D/D, rhythmicity persisted throughout the entire period of exposure to D/D (Fig. 3). Clear free-running rhythms were seen in 9 out of 10 animals in D/D with an average Tau of 24.2±0.3 h. Alpha, the length of the main bout of activity, was significantly longer (paired t-test, p<0.03) in D/D (12.5±0.9 h) than in L/D (9.5±0.6 h) (Fig. 4B).

While significant free running rhythms were also observed in all animals exposed to L/L, the clarity of the rhythms was diminished. Overall, the average free-running period in L/L was 23.5±0.6 h. The Tau values in L/D, D/D, and L/L were not statistically different (F test, p>0.4). There was no effect of sex on Tau, overall activity, alphas or phase angles (unpaired t-tests, p>0.05).

In the running wheels, the overall distances traveled in L/D (50.1±12.3 m/day), D/D (85.4±20.0 m/day), and L/L (54.6±11.5 m/day) were statistically indistinguishable (Fig. 4C; Repeated measures ANOVA, p>0.3). There was also no significant

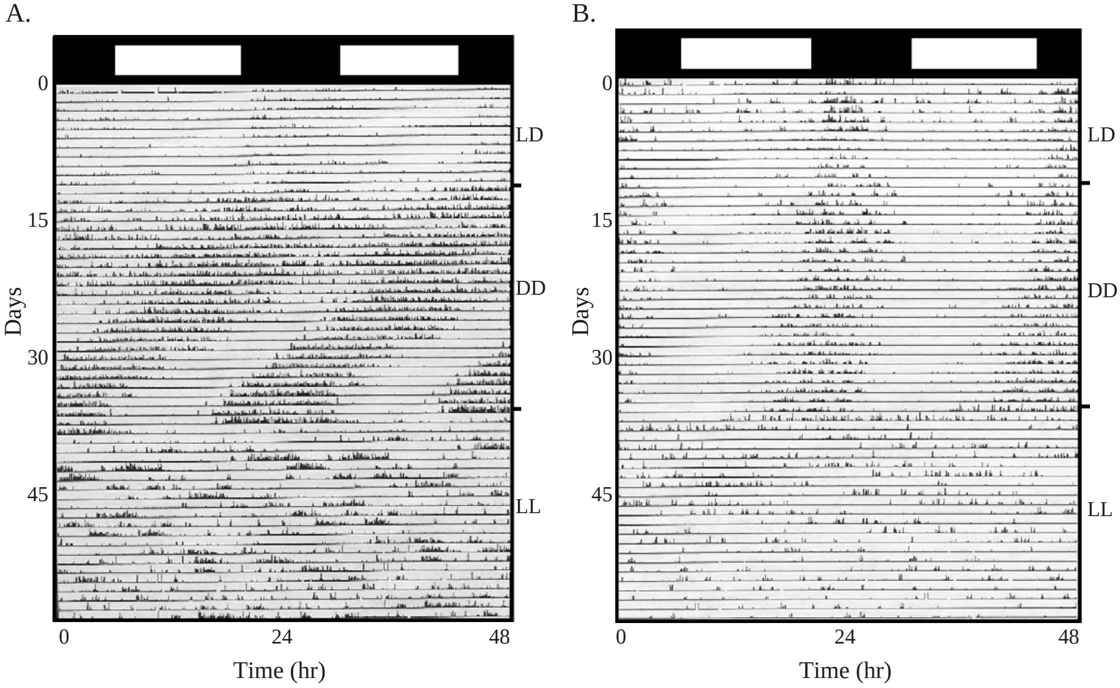

Fig. 3. Running wheel activity in L/D, D/D, and L/L plotted in 5 min bins for 2 representative lobsters (A and B). Periodogram analyses produced calculated periods of 23.80 and 24.05 h for these lobsters in L/D (see Fig. 4A), indicating entrainment to the L/D cycle. When in D/D, free running rhythms were apparent with Tau values of 22.83 and 23.85 h, respectively. (Note that black bars at top of figure=dark (D); white bars=light (L); maximum scale for individual days—A=6.0 m, B=4.6 m; and the data are double-plotted).

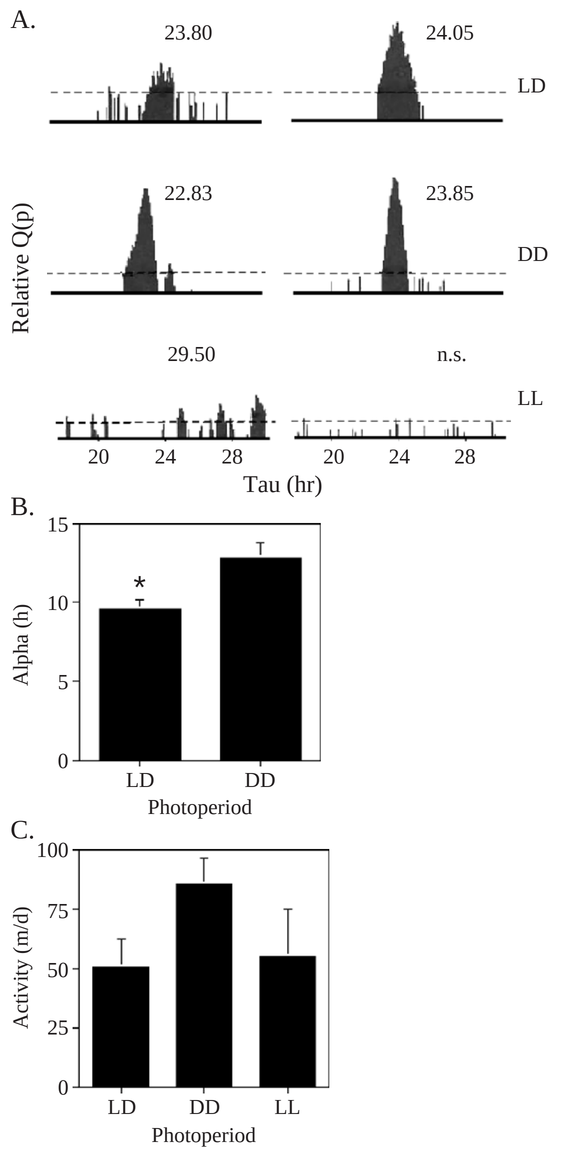

Fig. 4. Circadian rhythm analyses of running wheel activity data. (A) Periodogram analyses of the lobster activity shown in Fig. 3 (A on left, B on right). Separate analyses were performed for each lobster for each photoperiod condition. Peaks above the dotted lines are significant at $p<0.05$. The values for the highest peaks (Best Tau) are included above each periodogram. (n.s. indicates not significant). (B) The effects of photoperiod on the length of the main bout of activity, Alpha. The main bout of activity is significantly longer under D/D than L/D conditions. (C) The effects of L/D, D/D and L/L on cumulative amounts of activity/day. There was no statistically significant difference in daily levels of activity in dark/dark (D/D), light/dark (L/D) or light/light (L/L) conditions. Values are plotted as mean±S.E.M. for all lobsters ($n=10$) (* indicates $p<0.05$).

difference between the distance traveled by lobsters in running wheels under L/D conditions and distance traveled by lobsters in racetracks exposed to ambient L/D conditions (60.1±6.5 m/day) (unpaired *t*-test, $p=0.12$).

4. Discussion

Long-term trials with running wheels in constant darkness provide clear evidence that *H. americanus* possesses an endogenous circadian clock that influences locomotor activity with a tendency to be most active at night. However, comparisons between activity patterns in the running wheels vs. racetracks suggest that this endogenous rhythm may be strongly influenced by environmental cues or the internal state of lobsters because a large proportion of the lobsters exposed to ambient conditions in the racetracks did not express an apparent rhythm. Recent locomotion data obtained using ultrasonic telemetry from freely behaving lobsters in their natural habitat further support this conclusion (Golet et al., submitted for publication). In that study, 23 of 25 lobsters were just as active during the day as during the night. Similarly, in another companion study, we compared locomotor activity recorded from lobsters in racetracks in the field with lobsters in racetracks of the same design in the laboratory (Jury et al., in preparation). In these field trials, consistently high levels of daytime activity were also evident even though the overall level of activity was generally higher at night. Therefore, while the present study clearly demonstrates the existence of an endogenous circadian clock in *H. americanus*, the extent to which this clock influences normal behavior in the field is not clear.

Evidence for an endogenous component to the activity rhythms of lobsters is consistent with prior reports explicitly testing circadian rhythmicity in this species (Cobb, 1969). However, while Cobb (1969) demonstrated that a nocturnal pattern of activity persisted in D/D conditions, his results were not completely compelling because the flow-through seawater systems in his study could have been providing some type of exogenous cue that synchronized the behavior. In the present study lobsters in running wheels under D/D and L/L conditions received no exogenous cues because they were in environmentally controlled recirculating aquaria. Nevertheless, under these conditions, a consistent drifting free running circadian rhythm was demonstrated. Interestingly, while the data obtained from lobsters in racetracks were consistent with a circadian pattern of activity entrained to photoperiod, there was little indication of a tidal rhythm despite the potential tidal cues provided by ambient changes in temperature and salinity in the flow-through tanks. The significantly longer alpha in D/D compared to L/D, without a significant increase in overall activity in D/D (Fig. 4B), also suggests that locomotor activity is occurring over longer periods in individuals under constant darkness when there is no inhibition of activity by exogenous light cues.

The techniques used in the present study have several advantages over other methods used to measure crustacean locomotion. First, the use of magnetic devices to detect activity removes the effect of variability in light levels and/or turbidity on recordings (Krum and Sheehan, 1992). Second, additional lighting, which may affect behavior, is not necessary as in some techniques (i.e., video). Even infrared light, which lobsters probably do not detect (Jury et al., 2001), does not readily penetrate seawater and thus it is not very practical for many marine applications. Third, both the racetrack and running wheel systems are relatively inexpensive and readily adaptable to field use; making it possible to deploy a number of units in a variety of habitats (Jury et al., in preparation). Finally, in contrast to many techniques that only measure relative change in activity, both methods used in this study measure actual distance traveled.

A potential criticism of these methods is, while magnetoreception per se has not been documented for *H. americanus*, some lobsters (e.g., *Panulirus argus*) appear to possess the ability to detect magnetic fields (Lohmann et al., 1995; Wiltschko and Wiltschko, 1995; Boles and Lohmann, 2003). Thus, while magnets may potentially influence lobster activity in some way, it is unlikely that this affected our results for the following reasons: First, experiments conducted with video controls did not show any differences between magnet and non-magnet trials, in terms of overt behavior and distance traveled (data not shown). Second, we only monitored the distance traveled, not the direction of movement. Thus orientation, even if altered by the magnet, would not have affected our results. Finally, our data compare favorably to the timing and magnitude of activity seen in other published studies of *Homarus* spp. using “non-magnetic” methods (Cobb, 1969; Lawton, 1987; Karnofsky et al., 1989; Smith et al., 1998, 1999).

In conclusion, an endogenous circadian rhythmicity exists in *H. americanus*, but there appears to be extensive variability in the actual expression of locomotor activity patterns under ambient conditions. Thus, the timing and magnitude of the locomotor activity of lobsters in their natural environment is probably due to their responses to exogenous environmental stimuli superimposed upon an endogenous pattern determined by an internal timer (Rebach, 1987; Williams and Dean, 1989). This combination of the influence of exogenous and endogenous components has been observed in several decapod crustaceans, and this plasticity of behavioral response may be adaptive due to the range of habitats utilized by this species (Arechiga and Rodriguez-Sosa, 1997).

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