ICES Journal of
Marine Science

Into a rhythm: diel activity patterns and behaviour in Mediterranean slipper lobsters, *Scyllarides latus*

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Although the natural history for Mediterranean slipper lobsters (*Scyllarides latus*) is well established, there exists a disproportionate lack of important biological and physiological data to verify many key traits, including to what extent endogenous rhythms modulate aspects of their behaviour. Although Scyllarids appear nocturnally active, few studies exist that quantify this tendency. Our overall objective was to test the hypothesis that adult slipper lobsters are nocturnal and to determine if their diel activity rhythms are under the influence of an endogenous circadian clock. In the laboratory, we exposed a total of 16 animals ($CL_{avg} = 92.6 \pm 6.6$ mm; CL, carapace length) to a 12 : 12 light : dark (LD) cycle for 7 – 10 d, followed by ***constant dark (DD) for 15 – 20 d. Activity was assessed using a combination of time-lapse video and accelerometers. Of a total of 16 lobsters, we analysed data from 15 (one mortality). All 15 lobsters were evaluated using video. Thirteen of these lobsters were also evaluated using accelerometers. All lobsters were more active during night-time than during daytime and synchronized their activity to the LD cycle, expressing a diel activity pattern ($\tau = 24.04 \pm 0.13$ h). In DD, lobsters maintained a circadian rhythm with a τ of 23.87 ± 0.07 h. These findings may provide insight into the behaviour of these animals in their natural habitat and help explain their ability to anticipate dawn and dusk.

Keywords: biological clock, circadian, endogenous rhythms, light – dark cycles, scyllaridae.

Introduction

In many marine crustaceans, rhythmic behaviours such as foraging, locomotion, and overall activity are often associated with the synchronization and modulation by circadian clocks (Naylor, 1988, 2005; reviewed in Arechiga et al., 1993). These rhythms are strongly influenced by environmental factors, most notably light (Arechiga and Rodriguez-Sosa, 1997; reviewed in Golombek and Rosenstein, 2010). Endogenous rhythms have been described for a variety of marine crustaceans (reviewed in Arechiga and Rodriguez-Sosa, 1997) including crabs (Palmer, 1995; Forward et al., 2003), shrimps (Adhub-Al and Naylor, 1975; Matthews et al., 1991), isopods (Bohli-Abderrazak et al., 2012), amphipods (Rossano et al., 2008), and copepods (Hough and Naylor, 1992). With respect to lobsters, there are representative studies of activity rhythms and locomotion of two general groups: spiny lobsters (e.g. *Panulirus argus*; Lipcius and Herrnkind, 1982, 1985) and

clawed lobsters (e.g. *Homarus americanus*; Jury et al., 2005). For example, Atkinson and Naylor (1976) and Aguzzi et al. (2003, 2004) established the presence of endogenous rhythms in Norwegian lobsters, *Nephrops norvegicus*, and the potential alterations to these activities based on light-limiting habitats (i.e. the continental slope). Jury et al. (2005) demonstrated that American lobsters, *H. americanus*, were strongly influenced by an endogenous circadian clock in both racetrack and running wheel laboratory trials; however, there was large variability in this pattern. In a subsequent study, Golet et al. (2006) concluded that the variation in the expression of diel *in situ* activity patterns might be driven by changes in natural habitat, altering these predominantly nocturnal behaviours. Two other spiny lobster species, *Jasus edwardsii* and *Panulirus japonicus*, appear to exhibit strong, persistent rhythms (under constant conditions) and are likely under the control of an endogenous circadian clock (Williams and Dean, 1989;

Nagata and Koike, 1997). In the latter species, direct and consistent exposures to light can override the circadian clock, creating variation in locomotive activity among individuals. This phenomenon has also been shown in other marine arthropods (e.g. horseshoe crabs; Chabot *et al.*, 2007). Therefore, while it is assumed that many lobsters possess a nocturnal bias in their overall activity, the behavioural output of these patterns can be flexible.

A third and major group of lobsters, the Scyllarids (slipper lobsters), also appear nocturnally active. However, the prevalence of endogenous rhythms in slipper lobsters remains elusive (see Lavalli *et al.*, 2007). Mediterranean slipper lobsters (*Scyllarides latus*) exemplify a commercially and biologically important species throughout their range. *Scyllarides latus* are formidable, highly mobile marine decapods that inhabit both shallow and relatively deep areas (4–100 m) of the Mediterranean Sea and eastern Atlantic Ocean from the mainland coasts of Portugal south to Gambia and the islands of Madeira, the Azores, and Cape Verde (Holthuis, 1991; Spanier and Lavalli, 1998). *Scyllarides latus* are capable of attaining sizes >100 mm carapace length (CL) and weights of 1.5 kg (Martins, 1985) and are the target of a selective, but overexploited, fishery throughout their range (reviewed in Spanier and Lavalli, 1998). Recently, this species has been listed under the IUCN Red List of Threatened Species and is designated as "data deficient" (http://www.iucnredlist.org/details/169983/0).

Although the natural history for *S. latus* has been largely disseminated, there remains a lack of important biological and physiological data to substantiate many key behavioural traits, including to what extent endogenous rhythms modulate locomotion and activity (Spanier and Lavalli, 1998; Pessani and Mura, 2007). Tangential studies suggest these animals display strong nocturnal behaviour indicative of an endogenous circadian rhythm (Spanier *et al.*, 1988; Spanier and Almog-Shtayer, 1992); however, this has not been fully substantiated. Adult *S. latus* are found mainly on hard substrata and rocky outcroppings in coastal waters; sheltering during the day on the ceilings of highly recessed caves or crevices with minimal light (Spanier and Almog-Shtayer, 1992; Barshaw and Spanier, 1994). Some discrepancies in the display of nocturnal behaviour have been noted in laboratory settings, especially in the absence of predators, resulting in a shift toward more diurnal activity (Barshaw and Spanier, 1994). Interestingly, for the ~88 species of Scyllarids known, there is only one study that has formally described endogenous rhythms. Jones (1988) provided the most detailed analysis of diel activity patterns for two shallow-water Scyllarid species (*Thenus indicus* and *T. orientalis*), which varied from diel to nocturnal behaviours under naturalistic aquarium conditions. Based on these contrasting patterns, the primary goal of the present study was to provide better resolution of the activity patterns in *S. latus* during LD cycles. Our hypothesis was that *S. latus* are nocturnal under simulated LD periods and continue to display this behaviour under constant conditions, suggestive of a circadian rhythm. We further postulate that such behaviours are adaptive and advantageous to an animal that relies on cryptic behaviour and low-light conditions to avoid predation.

Our approach was to use accelerometry as a tool for quantifying the long-term activity associated with endogenous rhythms in *S. latus*. The use of accelerometers is becoming widespread and serves as a relatively low-cost, but highly effective method and has been employed for other species of lobsters (clawed, *H. americanus*, Lyons *et al.*, 2013 and spiny, *P. argus*, Gutzler and Butler, 2014) and allows for the collection of large datasets that can record activity patterns and movement. We utilized time-lapse video recordings to help ground-truth the accelerometer data, as well as to observe other behaviours associated with endogenous rhythms.

Materials and methods
Animal acquisition and environmental conditions
Adult, intermolt slipper lobsters used for this study ($n = 16$, $CL_{avg} = 94.6 \pm 2.0$ mm; CL range = 81–105 mm) were obtained two ways: (i) at a local fish market in in Akko (Acre, northern Israel, N 32°.9331; W 35°.0827) where they were caught by fishers*** using trammel nets in shallow (5–10 m) coastal areas and obtained within 24 h of capture and (ii) using SCUBA in the same vicinity. The lobsters were captured in the early summer before the migration to cooler waters offshore (Spanier and Lavalli, 1998). All lobsters were transported in coolers to the marine biological laboratory at the Leon Recanati Institute for Maritime Studies, University of Haifa where they were used in activity assays within 2–3 weeks. Animals of both sexes (11 males and 5 females) were held communally in tanks with shelters in ambient seawater (20–22°C, 40 psu salinity) and exposed to a 12 : 12 h light : dark (LD) cycle and fed weekly a combination of bivalves (*Spondylus spinosus*) and limpets (*Patella caerulea*). Daytime light levels were produced by full-spectrum lights (Ikea Sparsam model 1230, 7 W, 45 lm/W) at an intensity of 185 ± 0.64 lux (mean $\pm$ standard error of the mean (s.e.m.), ~5.55 μmol photons/m^2/s, $n = 750$ readings) during the day and 2.4 ± 0.21 lux (~0.072 μmol photons/m^2/s, $n = 750$ readings,) at night. Light levels were measured using a Vernier Labquest Mini system with light sensor (LS-BTA, Vernier Technology Co.). We determined ecologically appropriate light intensities for our holding tanks and trial simulations in a preliminary study by securing HOBO light loggers *in situ* ($n = 3$, model UA0200, Onset Computer Corp., Bourne, MA, USA) to the entrances of lobster dens at a depth of 10–15 m (close to the lobster capture site). The sensors were left for two weeks after which they were retrieved and the data downloaded.

Experimental setup
Two activity arenas ($60 \times 40 \times 24$ cm ($L \times W \times H$), 57L, one lobster/arena) were used for all trials and placed next to each other, separated by an opaque divider, in a light-tight, climate-controlled room. Before each trial, lobsters were fed to satiation. Each arena included a round opaque PVC shelter (16 cm diameter) that provided shelter and shade. Tanks were fitted with a filter system (Mignon filter 60, AZOO) that allowed each tank (replicate) to run as a closed system. Full-spectrum lighting was used and temperature and light levels were maintained at levels described above. For the first 8–10 d, lobsters in each trial were subjected to 12 : 12 LD cycles, controlled by a digital timer (Hyundai BND-50/IS8) programmed to a current exogenous sunrise–sunset schedule. All light and temperature levels were recorded using HOBO Pendant temperature–light loggers in 15-min intervals. After this initial 8–10 d period, lobsters were exposed to constant darkness (DD) for an average of 17 ± 0.63 d. During this time, infrared lighting (embedded in the camera and chosen for its minimal influence on the visual sensitivity in crustaceans, inclusive to lobsters; Bruno *et al.*, 1977) was used to illuminate animal activity.

Activity assessment using video
Overall, lobster activity was recorded using a colour day–night infrared-enabled CCD camera (PC177IRHR08, SuperCircuits, Austin, TX, USA) mounted above the activity arenas. The camera

output was then digitized (Canopus ADV5, Grass Valley, Hillsboro, OR, USA) and archived to a computer (Macmini, OS 10.5.6, Cupertino, CA, USA) using video capture software (Gawker, v. 0.8.4, Seattle, WA, USA) that date–time stamped and recorded the video at 24 FPS with a picture captured at each 15-s interval (240 data points per hour). A subset of videos, categorized into 1-h time blocks, were analysed using Windows Media Player Classic (v.1.2.1008). Activity was defined as forward, backward, or sideways locomotion (>2 cm) for each lobster. We also observed neutral behaviours (seen in the video and detected by the accelerometers), such as den-maintenance or antennal flicking. However, these behaviours were excluded from data analyses as they did not meet the threshold for activity, which was quantified as locomotion rather than neutral behaviours. Activity was recorded per hour by counting each minute during an hour the lobster was active. Minutes active per hour were averaged over each light and dark period (per 24-h calendar day) to give an average percentage of time active per hour. Average time active per light or dark period (per animal) were compared using a Student's *t*-test. During video analysis, we also made notes of other behaviours (e.g. digging, climbing, etc.). The video data also served as a backup in the event of any issues with the accelerometers.

Activity assessment using accelerometers

Concurrent with the video recordings, 13 of the original 16 lobsters were fitted with an accelerometer (HOBO Pendant G, model: UA-004-64, Onset Computer Corp., Bourne, MA, USA) capable of recording and storing movement and activity over a three-axis range at a high resolution (± 3G). Accelerometers were fastened to each lobster using a custom-built harness consisting of a curved platform (~ 9.4 cm^2) with two embedded cable ties. The harness was cemented, using a two-part putty-epoxy (AquaMend, Polymeric Systems Inc., Elverson, PA, USA), to the dorsal carapace of each animal and then sealed with liquid epoxy (Figure 1). This configuration allowed the loggers to be easily removed, downloaded, and re-fastened at weekly intervals with minimal disturbance to the animals. Activity data were recorded by each accelerometer every 30 s. Data were analysed to determine a threshold for activity, as the accelerometer was capable of picking up subtle
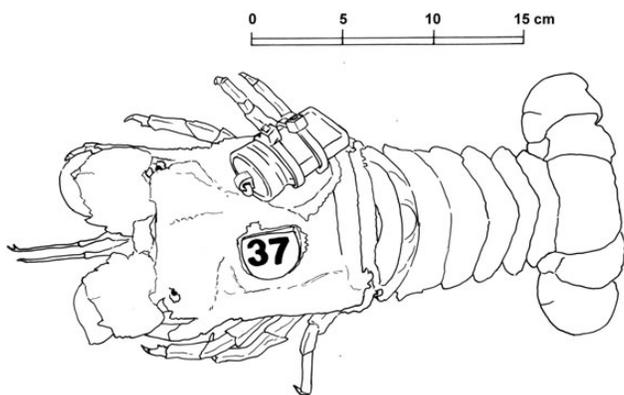
movements in lobsters (e.g. twitching and antennal behaviours) that we did not consider activity (see Table 1 in Barshaw and Spanier, 1994) and therefore filtered out. The accelerometer data were plotted and analysed as actograms and Lomb-Scargle periodograms ($p < 0.05$) using ClockLab® (MatLab, Actimetrics, Evanston, IL, USA, v. R2009a), as described in Dubofsky *et al.* (2013). The evaluation of peaks (10–30 h) in the periodogram was used to determine if the animals expressed a circadian (~ 24 h) rhythm and visual inspection of each actogram was also used to substantiate data from the periodograms. Significant differences in activity level during the day and night were determined for animals that expressed a diel rhythm in LD. Cumulative total activity (per cent active per hour during light and dark hours) was calculated for the entire trial period and analysed using a Student's *t*-test. All data were analysed using JMP Pro v.11.0 (SAS Institute, Inc., Cary, NC, USA) and represented $\pm$ s.e.m. unless otherwise noted.

Results

Of a total of 16 lobsters, we analysed data from 15 (one mortality). All 15 lobsters were evaluated using video. Thirteen of these lobsters were also evaluated using accelerometers. Due to technical difficulties, two of the replicates did not provide accelerometer data. Furthermore, we also determined if there were any sex-related behavioural differences. We used a series of *t*-tests to compare males ($n = 11$) and females ($n = 5$) for both overall activity in light ($p = 0.94$) and dark ($p = 0.55$) as well as periodogram data (τ values, LD, $p = 0.37$; and DD, $p = 0.08$); no significant differences between males and females were apparent. The variable τ represents the length of the activity rhythm.

Video data

Of the 15 lobsters for which we had video, we analysed a subset ($n = 6$) of individuals due to time restraints. However, we felt that this was a representative sample, especially when we compared these data with those from our periodogram analyses (completed for 13 animals). During LD, lobsters were observed to be nocturnal (Figure 2) which appeared to continue as a circadian rhythm
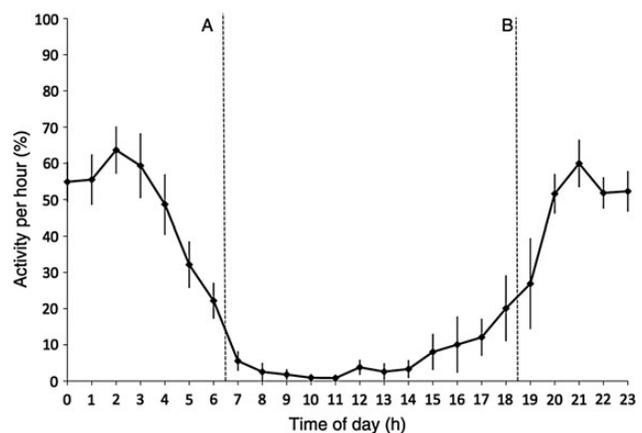

Figure 1. An accelerometer unit and mounting harness cemented to the dorsal side of a Mediterranean slipper lobster, *S. latus*. The accelerometer was used for quantifying movement activity during both light:dark (LD) and constant dark (DD) conditions. Data were collected at 30 s intervals; the accelerometer was removed and re-attached at weekly intervals (see Methods for details).

Figure 2. Average activity per hour over a 24-h period for six lobsters (*S. latus*) over 9.33 $\pm$ 0.56 days (the entire LD period for each lobster). Data were collected via video. Over the 24 h period, we combined lobster activity into four periods: (i) 07:00 – 14:00, (ii) 15:00 – 19:00, (iii) 20:00 – 03:00, and (iv) 04:00 – 06:00 corresponding to daytime, sunset, night, and sunrise. The dashed vertical line "A" indicates sunrise (06:30), dashed vertical line "B" indicates sunset (18:30). Activity between all four times was significantly different (ANOVA; $p < 0.001$).

during the DD period (17 ± 0.63 d, active 47% of night-time vs. 14% of daytime).

Over the 24-h cycle, we combined lobster activity into four periods: (i) 07:00–14:00, (ii) 15:00–19:00, (iii) 20:00–03:00, and (iv) 04:00–06:00 corresponding to daytime, sunset, night-time, and sunrise. Activity during these times was significantly different ($n = 6$, ANOVA; $F_{3, 140} = 116.5$, $MS = 24710.8$, $p < .001$, Figure 2). Additionally, lobsters displayed markedly different activity levels between any of the given four periods (Tukey HSD; $q = 2.60$, $p < 0.02$, $\alpha = 0.05$, Figure 2). For example, between the hours of 20:00 and 03:00 lobsters were more active (mean = $56.1 \pm 2.6\%$) compared with activity between 07:00 and 14:00 (mean = $2.6 \pm 2.1\%$).

In addition to forward, backward, or sideways locomotion, we noted a variety of other activities, including grooming, waving (slow repetitive rocking movements), and antennal flicking (see Supplementary Video, Barshaw and Spanier, 1994, Table 1). These neutral behaviours also appeared to increase in frequency as sunset approached and decreased before sunrise (see Supplementary Video). When comparing video and accelerometer activity data, we found no significant difference between the two methods of collecting activity data (Pearson's correlation, $p < 0.0001$, $R^2_{adj} = 0.898$, Figure 3).

Accelerometer data

All 13 lobsters expressed a diel rhythm of activity when exposed to a LD cycle ($\tau = 23.96 \pm 0.318$ h, Figure 4). In addition, 12 of the 13 lobsters displayed significantly more activity at night during the LD cycle (t-test, $d.f. = 11, 7$, $p \leq 0.01$, Figure 5). The remaining lobster still showed a circadian trend ($\tau = 24.75$ h, actogram not shown); however, this animal appeared to express an increased level of activity during the day. Overall, lobsters were active $59.05 \pm 1.37\%$ per hour at night vs. $40.35 \pm 1.56\%$ per hour during the day. In constant conditions (DD), all lobsters expressed a circadian rhythm of activity ($\tau = 23.85 \pm 0.134$ h, Figure 4).

Because their endogenous rhythms were shorter than 24 h, lobsters became active earlier with each consecutive day in DD (Figure 4).

Discussion

Our results provide the first evidence that the diel rhythm of activity in Mediterranean slipper lobsters, *S. latus*, is controlled by an endogenous clock (Figure 4). After synchronizing their activity patterns to an imposed LD cycle, these lobsters continued to express the same activity pattern in constant conditions, maintaining a circadian rhythm for the duration of the trial (Figures 4 and 5). Few studies have examined diel activity patterns in Scyllarid lobsters despite their economic and ecological importance throughout their range (Lavalli *et al.*, 2007). Jones (1988) has provided the only other detailed analysis of diel activity patterns for Scyllarid species (*T. indicus* and *T. orientalis*). Interestingly, our study animals demonstrated more activity during the day than expected, some of which was associated with grooming and den-maintenance behaviours. Both evaluative methods (video and accelerometer) showed a baseline of activity along with neutral movements during the day, but were significantly different from activity at night (Figures 2 and 5).

Our goal was to examine activity rhythms in both LD and DD without the influence of any other exogenous cues (e.g. predators, chemical cues, etc.) besides light. Although other laboratory studies suggest the shifting of *S. latus* to a diurnal rhythm when predators are not encountered (Barshaw and Spanier, 1994), we did not see this kind of behaviour. Our trials were focused on assessing individual activity patterns despite the propensity of this species to cohabitate with conspecifics. Previous studies of group behaviour may have different outcomes (Barshaw and Spanier, 1994), accounting for results that may differ from this study. In daytime field surveys by Spanier and Almog-Shtayer (1992), >50% of lobsters censused were found in dens or artificial reefs cohabitating with conspecifics. The influence of conspecifics and predators and their effects on circadian rhythms is still not well understood.
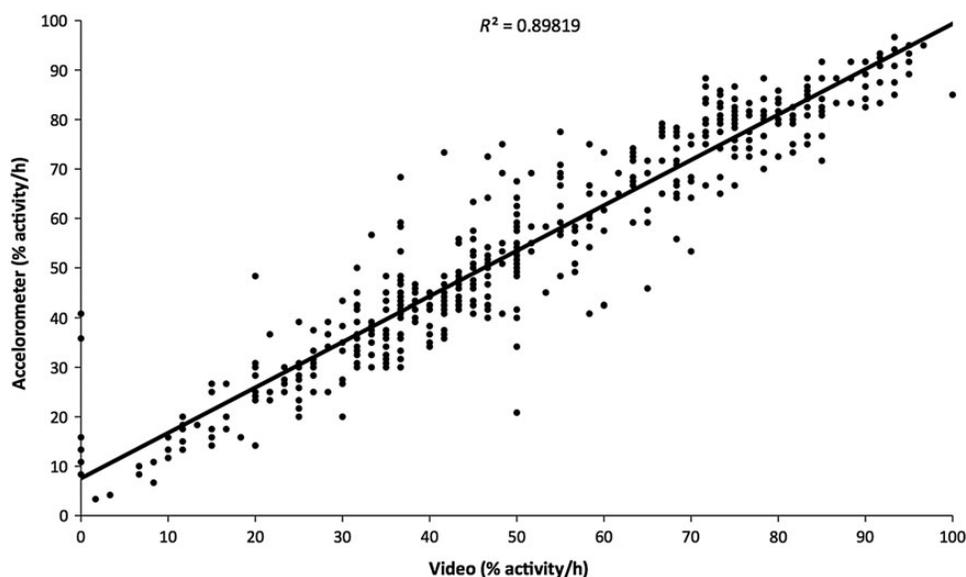
Figure 3. A methodological comparison between lobster (*S. latus*) activity measured using accelerometry and video analysis. The relationship between video and accelerometer data for an individual lobster over the entire testing period. There was no significant difference between the two methods of collecting activity data (Pearson's correlation, $p < 0.0001$). $R^2_{adj} = 0.898$ (Video = $-2.115246 + 0.9779221*$Accel).
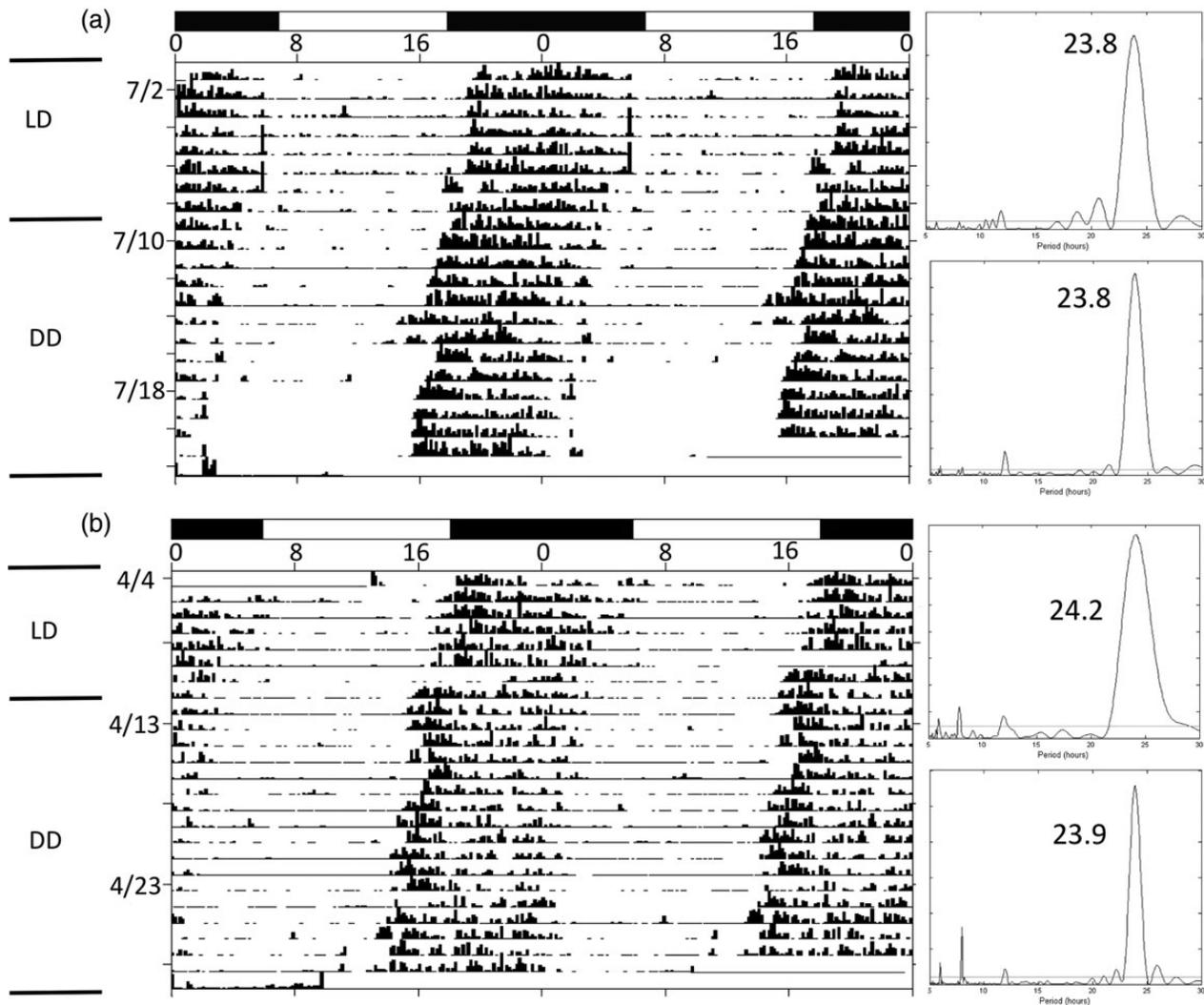
Figure 4. Characteristic locomotor activity recorded from two Mediterranean slipper lobsters (*S. latus*) during LD and DD periods of the study. Both animals showed a nocturnal pattern of activity including drifting during periods of DD. Each lobster was exposed to an imposed LD followed by DD, as indicated on left side of the figure. (a) LD = 9 days, DD = 16 days; (b) LD = 10 days, DD = 16 days. The imposed LD cycle is indicated at the top of the image; dark portions indicate night-time. Images on the left are double-plotted actograms, with periods of activity indicated by vertical black lines. Horizontal scale is time of day (hours) and activity is indicated in metre per second squared. Images on the right are Lomb-Scargle periodograms for the same animal during one of the two treatments (LD top, DD bottom). Vertical scale is the relative strength of rhythmicity ($Q(p)$); the horizontal scale is the period in hours (5–30); the largest peak above the horizontal line of significance ($p < 0.05$) is indicated by a numerical value.

Circadian rhythms are driven by internal biological clocks that have a period of ∼24 h, allowing animals to anticipate sunset and sunrise and, as a result, modulate changes in their behaviour or physiology (Naylor, 2005; Kronfeld-Schor *et al.*, 2013). Circadian clocks are typically entrained by external stimuli (light); however, they tend to persist in the absence of external cues. In the present study, we observed a noticeable increase of activity in our lobsters before sunset and an opposing decline in activity just before sunrise (Figure 2).

Adaptation to light

Scyllarides latus appear highly adapted to living in low-light environments and it is well known that these animals are found in dimly lit conditions, taking refuge in crevices and rocky outcrops

along coastal ridges (Spanier and Almog-Shtayer, 1992). Despite our simulated light levels being ∼5–10% stronger than what we measured *in situ*, all our animals exhibited a strong endogenous rhythm. How these lobsters sense and react to changes in light levels is not well known, although recent work by Lau *et al.* (2009) determined *S. latus* possess "superposition optics" (i.e. sensitivity to a light source affected by the number of facets by which light is collected and focused in the random) with respect to their vision that allows for a balance between optimal sensitivity and acuity. This optical mechanism is specifically adapted to dimly lit environments, and it is theorized that organisms equipped with superposition optics are excellent candidates for circadian rhythms (Lau *et al.*, 2009). We surmise that, like other nocturnal marine crustaceans, there is an increase in visual sensitivity that assists in prey
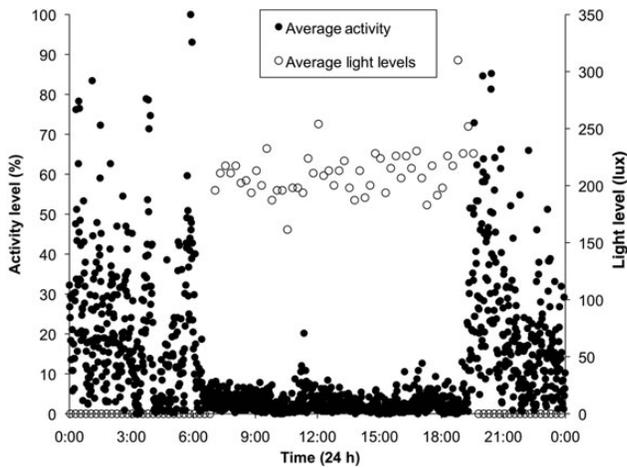
Figure 5. Comparison of average activity and light levels over 5 d for one lobster, *S. latus* (CL = 87 mm). Activity was recorded every 30 s via accelerometer. Average activity was calculated by summing the two activity readings per minute then averaging the sum per minute over five consecutive days. Activity per hour at night averaged 59.05 ± 1.37% and was significantly different from daytime activity per hour (40.35 ± 1.56%, $p < 0.01$). Light levels were recorded every 15 min (light sensor) and ranged from 0 to 350 lx (0 – 10.5 μmol photons/m^2/s). Overall, activity levels increased dramatically as light levels decreased.

capture or predator avoidance (Meyer-Rochow, 2001), which would be advantageous for lobsters like *S. latus* in their natural habitat. Furthermore, it is proposed that the synchronization of circadian rhythms through visual inputs provides an enhanced level of protection aiding in other activities (Meury and Gibson, 1990; Pizzatto *et al.*, 2008; Lee, 2010). Future work to assess the visual sensitivity of *S. latus* in relation to their activity (e.g. ERG assay, Watson *et al.*, 2008) and examining the role of circadian clocks would serve as a useful follow-up to this study.

Although the lobsters used in these trials were all obtained from relatively shallow locations (10–15 m), Mediterranean slipper lobsters are distributed throughout a gradient of depths, including areas of the continental slope >50 m. It is not known how *S. latus* obtained from greater depths might respond to LD cycles given the more weakened light intensities to which they are accustomed. Norwegian lobsters (*N. norvegicus*) are known to entrain to circadian rhythms (Aguzzi and Sarda, 2008) and have also been shown to vary their burrow emergence rates between dusk and dawn (Sbragaglia *et al.*, 2013). However in lab-based trials, exposure to varying light intensities (representative of depths from slope to shelf waters, 10–400 m), resulted in the lobsters switching from nocturnal to diel activity. This suggests that light intensity and composition help to modulate a "behavioural temporal niche" (Chiesa *et al.*, 2010).

Behavioural adaptations

Endogenous clocks in mobile but cryptic species, such as *S. latus*, provide a selective advantage by enabling them to anticipate environmental change and return to their den before the onset of unfavourable conditions (Naylor, 1988, 2005). It is proposed that, like spiny (Lipcius and Herrnkind, 1982) and clawed (Karnofsky *et al.*, 1989) lobsters, *S. latus* forage exclusively at night to reduce their encounter with diurnally active predators, including triggerfish and grouper (Martins, 1985; Barshaw and Spanier, 1994). Maintaining strong, consistent locomotor rhythms is an adaptive

trait to maximize foraging and predator avoidance. Because *S. latus* predominately reside in low-light habitats, possessing an endogenous rhythm is essential to regulate optimal times for foraging vs. sheltering.

The capacity to alter endogenous clocks has been shown in a variety of organisms and the timing and type of change depends on the circumstances that modify the existing rhythm. For example, age may cause cane toads (*Bufo marinus*) to switch from a nocturnal to a diel pattern of activity (Pizzatto *et al.*, 2008) while amphipods (*Orchestoidea tuberculata*) make a transition from a nocturnal to a crepuscular pattern of activity (Kennedy *et al.*, 2000). Both of these organisms alter activity rhythms to avoid predation, especially by adult conspecifics. These patterns are noticeable in some lobsters as well, for example, ovigerous *N. norvegicus* (when compared with non-ovigerous females) appear to decrease their range and duration of emergence from dens (Aguzzi *et al.*, 2007).

Ontogenetic changes in the rhythms of *S. latus* are not known. However, seasonal movements of coastal populations (Martins, 1985; Spanier *et al.*, 1988) suggest that modifications in activity may originate from physiological, neurological, or metabolic changes as opposed to endogenous clocks (Roenneberg and Merrow, 2002; Helm *et al.*, 2013). The initiation and environmental trigger(s) responsible for these seasonally-induced movements are unknown, but are theorized to include changes in temperature as well as photoperiod (Spanier *et al.*, 1988; Spanier and Lavalli, 1998), similar to what is observed in spiny lobsters (Herrnkind, 1983). Alternatively, circannual clocks may serve as the mechanism behind changes in temporal and spatial distributions as is evident in other species such as migratory birds (Gwinner, 1996). We collected and tested for evidence of circadian rhythms in *S. latus* over nonmigratory periods and purposefully used lobsters of intermolt phase to avoid potential biases. However, it would be of interest to investigate circannual rhythms and their zeitgebers that may be associated with migration, molting, or mating.

The establishment of a circadian rhythm in Mediterranean slipper lobsters is an important descriptor of behaviour in this species. Our results may be useful for investigating the timing of biological processes, seasonal migrations, and responses to changing environmental conditions due to global climate change.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Acknowledgements

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Handling editor: Howard Browman