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Influence of light, food and predator presence on the activity pattern of the European spiny lobster *Palinurus elephas*: An investigation using tri-axial accelerometers

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ABSTRACT

The knowledge of the activity pattern of marine organisms represents a crucial aspect in the studies on their ecology. In this paper, we used for the first time data from tri-axial accelerometers to provide an accurate description of the activity pattern of the European spiny lobster, *Palinurus elephas*. Sixteen lobsters (8 males, 8 females) were tagged with tri-axial accelerometers in order to monitor their activity in a mesocosm during four replicate trials. In each trial the lobsters were submitted to three treatments of the duration of one day each: exploration, presence of food and presence of a predator. The variance of roll body angle (VariRoll) was chosen among a number of available variables as a proxy of lobster activity during each treatment. The lobsters were more active during the night and in low-light hours than during the day. Moreover, they were i) more active without food or predator, ii) less active in the presence of a predator, iii) with an intermediate activity level (i.e. values of VariRoll) in the presence of food. Besides contributing to the knowledge of *P. elephas* ecology, the results of this study provide a new analytical method to describe activity patterns in slow-moving animals.

1. Introduction

Marine and terrestrial animals synchronize their activity pattern (that is the temporal distribution of a proxy of activity over the monitoring period) and behaviour to different endogenous and exogenous stimuli to increase their fitness to environmental conditions. Light/dark cycle, food availability, predator presence and internal clocks are among the main factors that affect the activity pattern in many species (Aréchiga and Rodríguez-Sosa, 1997; Reebs, 2002). Indeed, the knowledge of activity patterns represents a crucial aspect of animal ecology and is essential for planning efficient conservation measures for species and habitats (Jiao et al., 2018; Pilyugin et al., 2016).

Among the largest marine crustaceans, spiny lobsters are spread worldwide (Holthuis, 1991). They constitute a major component of many tropical and subtropical small-scale fisheries and play an important role in benthic community structuring as well (Boudreau and Worm, 2012). Despite their importance and although numerous studies have examined their life history (Acosta and Robertson, 2003; Groeneveld et al., 2006; Jernakoff, 1990) their fine scale activity remains poorly known to date.

The European spiny lobster, *Palinurus elephas* occurs in the northeastern Atlantic Ocean and in the Mediterranean Sea from a few meters down to about 200 m depth, more frequently found on rocky bottom substrata between 10 and 70 m (Holthuis, 1991). In the Mediterranean Sea, *P. elephas* is a valuable fishery resource subject to intense fishing (Goñi and Latrouite, 2005; Hunter, 1999). Its activity pattern is known to be influenced by environmental variables such as light (Miller, 1990) and food availability (Goñi and Latrouite, 2005) and to be driven by anti-predatory behaviour (Buscaino et al., 2011a). Giacalone et al. (2015) investigated the effect of light on *P. elephas* in NW Sicily using acoustic telemetry and found a diel activity pattern (24 h cycle) with the most intense movements during the night.

Octopuses are among the natural predators of spiny lobsters (Bouwma, 2006; Butler et al., 2006; Butler and Lear, 2009; Díaz et al., 2005; Harrington et al., 2006). As octopuses and lobsters co-occur in rocky habitats they also compete for the availability of refuges (Butler

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and Lear, 2009; Lear, 2004). For these reasons, the octopus-lobster interaction has been the object of several studies that describe attack and defence strategies during their encounters (Barshaw et al., 2003; Briones-Fourzán et al., 2008; Gristina et al., 2009). To minimize predation risk, which represents the primary source of natural mortality (Butler et al., 1997,2006), spiny lobsters have developed effective defence strategies such as: aggregation and cooperative defence sheltering (Butler et al., 1999; Dolan and Butler, 2006; Eggleston et al., 1997; Mintz et al., 1994), sound production (Buscaino et al., 2011a), and use of the spiny antennas (Buscaino et al., 2011b), which are often triggered by chemical cues released by predators and/or by injured conspecifics (Barshaw et al., 2003; Briones-Fourzán et al., 2006).

The need to adopt the most efficient defence or feeding strategies (i.e. a behavioural trade-off) in relation to environmental changes (Berger and Butler, 2001; Briones-Fourzán et al., 2008; Derby et al., 2001) may affect lobsters' daily activity pattern. Such behavioural trade-off could be displayed in fine scale movements which are difficult to detect using *in situ* techniques such as acoustic telemetry, underwater visual census or video recording. Recently, tri-axial accelerometers technology was successfully applied to lobsters with the aim of describing some behavioural states. Goldstein et al. (2015) investigated the diel activity pattern and circadian rhythm of the Mediterranean slipper lobster *Scyllarides latus*, while Lyons et al. (2013) used accelerometers to estimate the rate of energy consumption in the American lobster *Homarus americanus*. Accelerometers were also used to assess the sound emission in *H. americanus* (Henninger and Watson, 2005) and in *P. elephas* (Zenone et al., 2019) by characterizing the mechanical vibration of the carapace. As accelerometer data are strictly related to animal body movements and attitude along the three dimensions (x, y, z), through their use it is possible to quantify activities such as feeding, escaping, or swimming/walking and to describe different behavioural states (Gleiss et al., 2017; Landsman et al., 2015; Van Deurs et al., 2017). This technology has been successfully used in many other species to draw their activity pattern. Different variables derived from the dynamic component of raw acceleration have been defined as a proxy of activity (e.g. Overall dynamic body acceleration ODBA, Vector of dynamic body acceleration VeDBA: Mori et al., 2015; Wright et al., 2014; Lyons et al., 2013; Wilson et al., 2006), but less attention has been paid to variables derived from gravity and the static component of acceleration, like e.g. variance in pitch body angle (Chimienti et al., 2016). However, the choice of one of these derived variables to describe activity is strongly dependent on many factors such as the species and its behavioural pattern and activity levels, or the location of the accelerometer in the animal body (see Qasem et al., 2012 for an example of a proxy selection regarding the latter point). Indeed, an accurate testing should be performed in order to identify the variables that are most suitable as a proxy of activity from accelerometer data.

In this study we have used for the first time tri-axial accelerometers with the objective of describing the fine scale movements and the behavioural states of *P. elephas* in a mesocosm, in relation to: (i) daylight phase, (ii) food availability, (iii) presence of a natural predator. In order to achieve our goal, we first calculated and compared different variables and then we chose the one that better described activity in a slow moving animal such as the spiny lobster as a proxy of activity. In particular, we compared the most widely used dynamic acceleration proxies of activity (ODBA and VeDBA) with variances in body attitude (pitch and roll, derived from the static component of acceleration). We hypothesize that lobsters would change their daily activity pattern in the presence of food and of a predator. We expect that lobsters would decrease their activity remaining longer in their crevices in presence of a predator, while they would increase it while feeding and decrease it later during digestion.

2. Materials and methods

Twenty-six *P. elephas* individuals (13 males, 13 females) with 81.0 ± 5.2 mm mean carapace length were bought in July 2016, two months before the breeding season from the "Ittica Capo San Vito" enclosure (San Vito lo Capo, NW Sicily, Italy), which collects wild individuals from local fishermen and maintains them in large concrete tanks for sale. Due to the large number of specimens available at the enclosure we were able to select animals in good health conditions and in a post-moulting phase.

2.1. Experimental setting

The selected lobsters were transferred to the CNR-IAS facilities at Capo Granitola (SW Sicily) where two circular PVC tanks were set up for the experiment. Each tank was 250 cm in diameter and 4000 L in volume and was equipped with an independent flow-through seawater system from a common source. The two tanks (a storage and a mesocosm tank) were placed in an open space covered by a roof of nylon windbreak mesh in order to avoid direct insolation and to preserve the average 14L:10D natural July light cycle. All lobsters were kept in the storage tank without refuges and fed daily with a low amount of food in order to maintain them reactive. The mesocosm tank was provided with a thin layer of sea sand on the bottom, two rocky refuges with two crevices each and two rocky patches, in order to mimic as much as possible a natural environment (Fig. 1). Refuges and patches were built with stones taken from the sea with their natural biotic coverage.

2.2. Lobster tagging and experimental design

A total of sixteen healthy lobsters (8 males, 8 females) with 81.6 ± 5.5 mm carapace length were selected among the 26 individuals for the experiments. They were tagged with X16-mini Gulf

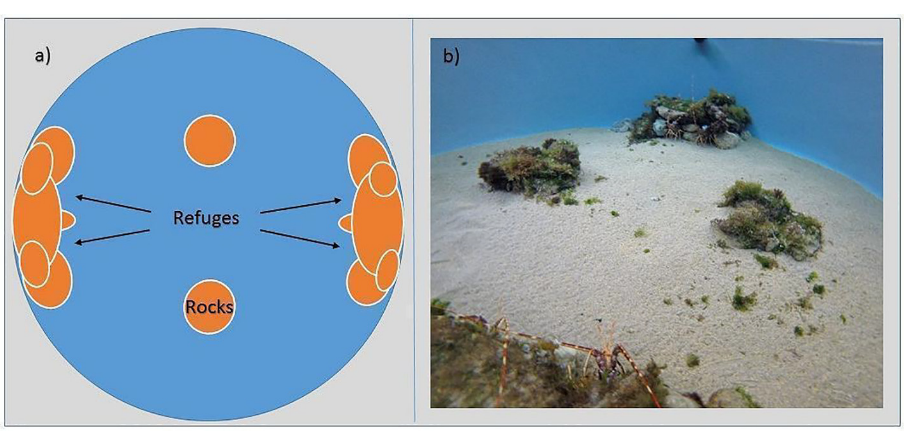

Fig. 1. Schematic representation (a) and underwater photo (b) of the mesocosm tank.

Coast Data Concepts tri-axial accelerometers (weight in air 17 g, weight in water 4 gr, i.e. < 2% of mean lobster weight) encapsulated in heat-shrink tube with enough air to achieve a slightly negative buoyancy of the whole package (Ciancio et al., 2016). Each device had an elliptical section of 25 × 13 mm and was glued on lobster carapaces using a quickly hardening epoxide resin. In order to visually recognize each individual, lobsters were marked with a different pattern on a small portion of the antenna using white nail varnish.

The experimental design took into account the following factors: Daylight phase (fixed with four levels: Sunrise from 5:00 to 6:00, Day from 6:00 to 20:00, Sunset from 20:00 to 21:00 and Night from 21:00 to 5:00); lobster Sex (fixed with two levels: Male, Female); Treatments (fixed with three levels: Exploration (Expl), Food (Fo), Predator (Pr)). During the Expl treatment (first day of each trial) lobsters were neither fed nor disturbed in any way. During the Fo treatment (second day) lobsters were fed with pieces of fish sunk at the centre of the tank. During the Pr treatment (third day) a predator, i.e. a common octopus *Octopus vulgaris* of ca. 500 g in weight was released into the tank and left there for 24 h.

Four trials of three consecutive days each (one day per treatment) were run in the mesocosm tank using four randomly-chosen lobsters (two males and two females) at each trial, in order to detect activity patterns during each 24 h cycle and to observe differences in behaviour during the different treatments. Each trial was preceded by a 4-hour acclimation phase to allow the lobsters to become familiar with the mesocosm tank and locate the refuges. During the acclimation phase videos were recorded using a GoPro camera (GoPro Inc., San Mateo, CA, US). Four hours of video footage extracted from a total of 16 h (4 h × 4 trials) were used for synchronization with the accelerometer data using time-specific calibrations (a repetitive motion was performed on each accelerometer at the beginning of the experiment). Accelerometer data were recorded continuously during all trials. Four different lobsters and the same predator were used in each trial. At the end of each trial the water within the mesocosm tank was fully renovated in order to remove any odour of lobsters and octopus and all food remains.

2.3. Data analysis

Raw acceleration data (surge, heave, sway) collected by the accelerometers were recorded at a 50 Hz frequency and used to determine when animals were active during the trials. In order to identify the best proxy of activity, the following derived variables were calculated from raw data: the overall body dynamic acceleration ODBA, the vectorial dynamic body acceleration VeDBA, pitch and roll body angles, variance (window 25 sec.) of pitch (VariPitch) and roll (VariRoll) angles. The acceleration data from each axis were then separated into their static and dynamic components following Shepard et al. (2008). Using the dynamic component of the acceleration we estimated the most frequently used proxies of activity and energy consumption "ODBA" and "VeDBA" (Qasem et al., 2012), a better proxy of activity when the orientation of the device is not aligned precisely with respect to the vertical. ODBA and VeDBA were given by:

$$ODBA = D_x + D_y + D_z$$

$$VeDBA = \sqrt{D_x^2 + D_y^2 + D_z^2}$$

where D represents the dynamic component of acceleration in: x longitudinal axis of the lobster, y lateral component, and z the dorso-ventral axis. Roll and pitch angles for each lobster were calculated by using the derived estimate of the gravity-based acceleration (i.e., static: Shepard et al., 2008):

$$Roll = a\sin(S_y)$$

$$Pitch = a\sin(S_x)$$

where S represents the static component of acceleration. VariPitch and VariRoll were calculated in order to amplify fine scale movements. As opposed to ODBA and VeDBA, that are sensitive to fast movements reflected in the dynamic component of acceleration but do not change much during slow movements, we expected that changes of body attitude during slow moving activity would be reflected in these two variables (VariPitch and VariRoll). The next steps were to choose the variable most sensitive to animal movement and to determine a threshold value to discriminate between an active and an inactive state. The noise produced by the instrument itself was first identified. Then different sections of data with active and inactive lobsters were extracted. To explore and compare different variables and identify the most suitable one in describing the lobster activity two of the simplest, as well as contrasting in terms of acceleration, behaviours were identified: "walking" and "still". "Walking" represented a lobster moving on the bottom of the tank, while "still" represented a resting individual. We visually inspected the signal of the four proxies of activity described before during these contrasting behaviors in order to choose its best proxy. After choosing VariRoll and a threshold for defining when the lobster is "active" a binary (0/1) variable was created (Active/Inactive, corresponding to a walking and a still lobster, respectively) and the frequency of active periods was calculated for each level of all factors.

To investigate the relationship between lobster activity and treatments, we applied generalised linear mixed-effect models (GLMMs) fitted with a binomial distribution with the function "glmer" of the "lme4" package of the R software (Zuur et al., 2009). We used individual lobsters as random effects to control for lack of independence between repeated measures over the same lobster. A backwards selection procedure (Crawley, 2007) was used to infer the significance of explanatory variables. We removed terms one by one following a decreasing level of complexity and we compared the models with and without the eliminated variable with the R function ANOVA using the Goodness-of-fit chi-squared test for GLMM and the Akaike information criterion (AIC) (Zuur et al., 2009). To compare between significant levels we used the Tukey's HSD post-hoc test. Before running the GLMMs we looked at temporal autocorrelation of data via autocorrelation plot of residuals after fitting a GLS model using the gls function of the nlme library in the R software (Zuur et al., 2009). This analysis showed a lag of 120 (2.4 sec.) data for which no autocorrelation was observed in the 50 Hz sample. For this reason, the data set was subsampled by removing 119 lines every 120 to decrease the autocorrelation and improve the computational power.

3. Results

The exploration and comparison of the variables pattern and their validation against the selected video footage led to the selection of VariRoll as the most suitable proxy of lobster activity. Neither ODBA nor VeDBA resulted suitable to detect slow movements, since walking and still lobsters produce similar signals from these two variables (Fig. 2). On the other hand, the variances in roll (VaRiroll) and pitch (VariPitch) angle showed a clearly distinct pattern between the two behavioural states (walking vs. still; Fig. 2). The value of the threshold chosen for VariRoll to detect lobster activity was 0.05. This value is lower than the median of VariRoll during "walking" and higher than the 3rd quartile of VariRoll during "still".

During the day VariRoll values were similar in all treatments (Fig. 3), with the exception of the predator treatment which disrupted the pattern observed in the other two treatments. At night the pattern of activity was different among treatments, mainly due to the presence of the predator which caused a decrease in VariRoll values in general, and the presence of food for which lobster showed a decrease in activity during the hours previous to the sunrise. The peak value recorded at 16:00 during the Pr treatment corresponds to the introduction of the octopus in the mesocosm tank, which was followed by a decrease in activity.

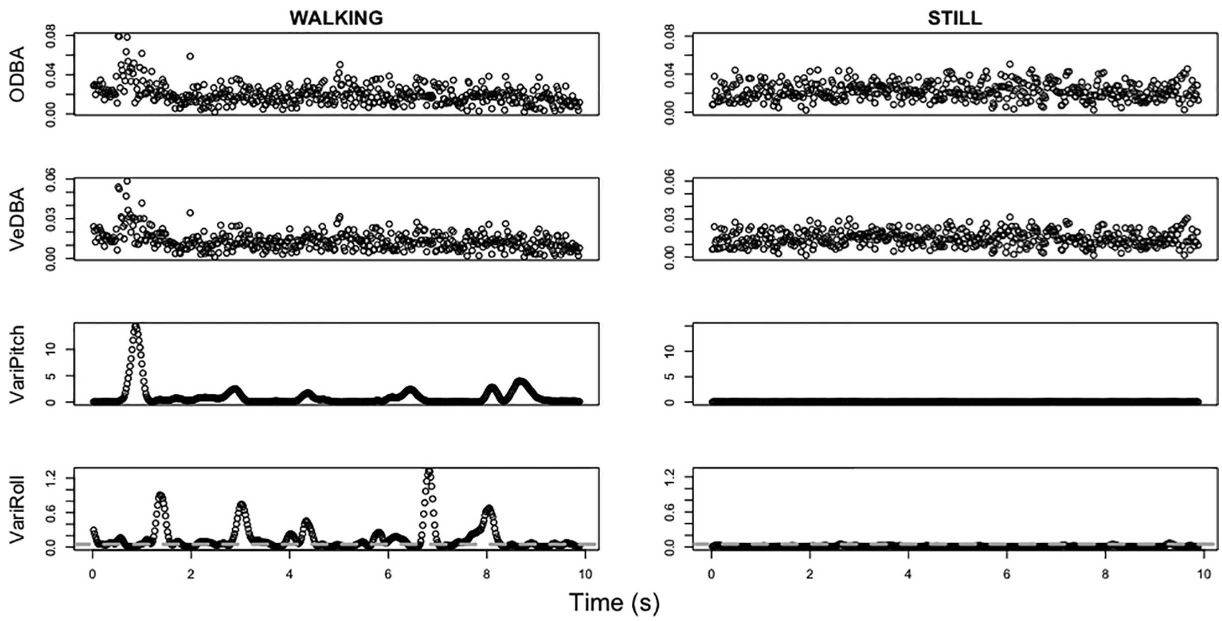

Fig. 2. Patterns of ODBA, VeDBA, VariPitch and VariRoll for a walking and a still lobster. The grey dotted line in the VariRoll graphs indicates the activity threshold chosen. The sampling frequency was set at 50 Hz.

The mean frequency of active periods (proportion of time spent active, i.e. with VariRoll values ≥ 0.05) recorded by the accelerometers of all lobsters in each daylight phase and during the three treatments is shown in Fig. 4. In the Expl treatment the frequency of activity is lower at sunrise and during the day compared to sunset and night. In the presence of food (Fo) the lowest and highest median values were recorded during day and sunset respectively. In the presence of the predator (Pr) the median values are similar during the different light phases, with a minimum at night.

The GLMMs selection procedure showed a significant effect of Daylight phase, Food and Predator on activity (VariRoll), but not of Sex (ANOVA function comparison between models with and without sex as explanatory variable, Table 1).

Lobsters expressed a diel rhythm as they were more active during the night and in low-light hours than during the day as a general effect (chosen model (b), Tukey HSD: day-sunrise: $z = -5.13$, $P < 0.001$; night-sunrise $z = 7.93$, $P < 0.001$; sunset-sunrise: $z = 8.12$, $P < 0.001$; night-day $z = 30.25$, $P < 0.001$; sunset-day $z = 16.10$, $P < 0.001$; sunset-night $z = 2.95$, $P = 0.05$).

Finally, lobsters displayed overall different patterns of activity during the three treatments (Tukey HSD: Fo-Expl: $z = -13.63$, $P < 0.001$; Pr-Expl: $z = -9.30$, $P < 0.001$; Pr-Fo: $z = 3.92$, $P < 0.001$).

4. Discussion

The present study provides detailed diel rhythms and activity patterns for the Mediterranean spiny lobster *P. elephas* described through acceleration data. The use of tri-axial accelerometers and the identification of the variance of the roll angle (VariRoll) as a suitable variable resulted as effective tools to provide an accurate description of lobster activity. Tagged lobsters were more active in the mesocosm during night and low-light hours. They were less active in the presence of the predator and the pattern of activity was influenced by the presence of food.

Nocturnal activity was previously documented for spiny and clawed lobster species (Goldstein et al., 2015; Bertelsen, 2013; Scopel et al., 2009; MacArthur et al., 2008) and for *P. elephas* (Giacalone et al., 2015). The latter authors, during an acoustic telemetry study conducted in summer on wild *P. elephas* inside a NW Sicily marine protected area, identified a periodicity of 24 h in their activity pattern with active movements between 20:00 and 06:00, which correspond to the most active phases found in the present study (sunset, night and sunrise). The retaining of diel rhythms in a mesocosm is common in several crustaceans (Watson et al., 2016; Jury et al., 2005) and it strongly suggests that our experimental findings mirror the free-living lobster behaviour.

The activity of lobsters decreased over the three treatments in the

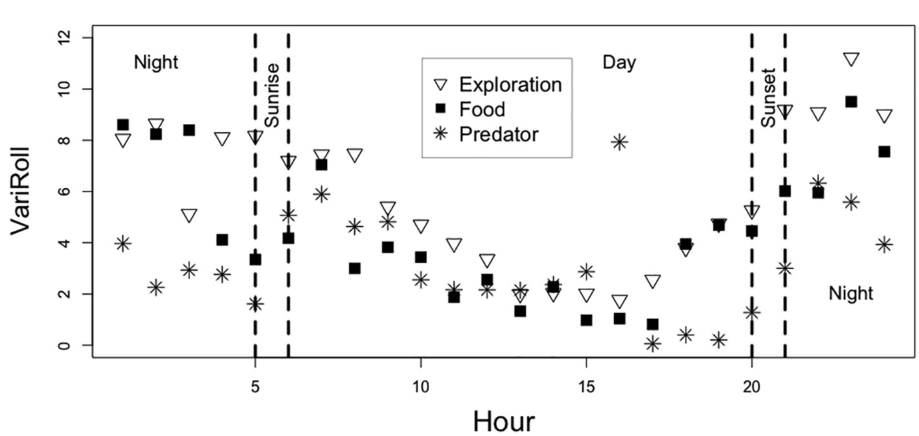

Fig. 3. Activity pattern across a 24 h cycle of the studied lobsters expressed as mean VariRoll values per hour in different daylight phases and different treatments.

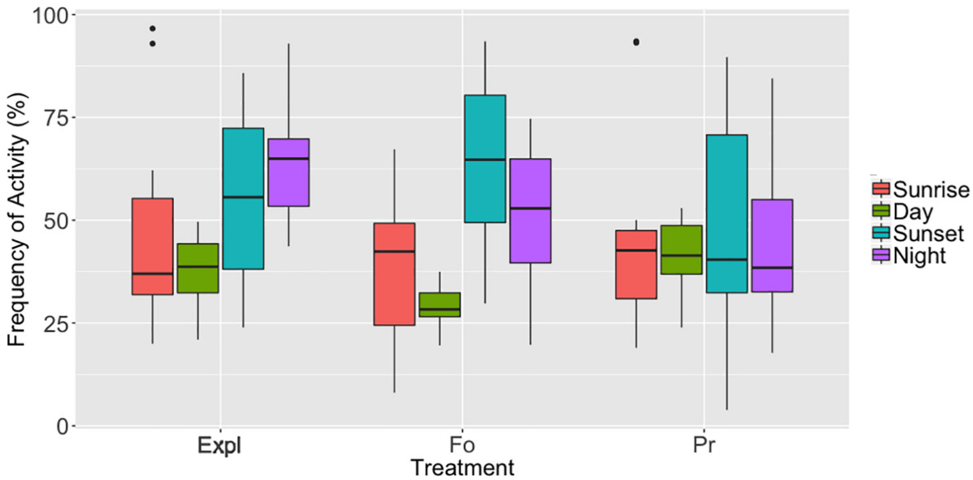

Fig. 4. Boxplots of the lobsters mean frequency of active periods (proportion of time spent active, i.e. VariRoll values ≥ 0.05) during the different light phases and in the different treatments. Expl = Exploration; Fo = Food; Pr = Predator.

Table 1
Model structures for activity as dependent variable, Akaike information criterion (AIC), and χ^2 values of residual deviances paired comparisons of the backwards selection procedure proposed for the GLMMs with the lowest AIC. The random effect structure is shown between brackets. Treatment refers to Exploration, Food, and Predator.

Model structures	DF	AIC	χ^2	P-value
a) sex + treatment + daylight phase + (1|lobster)	32,938	42983.5		
b) treatment + daylight phase + (1|lobster)	32,939	42981.9	0.39	0.53 (a &b)
c) daylight phase + (1|lobster)	32,941	43174.6		
d) treatment + (1|lobster)	32,942	44027.1		

following order: Exploration > Food > Predator. The highest activity recorded during the first 24 h (Exploration) is probably due to the exploration of the new environment, to the search for food, to the interaction with conspecifics and to the choice of a refuge. A similar behaviour was also previously reported by Giacalone et al. (2015,2006), when acoustically tagged lobsters started to move on the first day soon after their release at sea in a completely unknown natural environment. In addition, in our experiment lobsters were kept under a low-feeding regime in order to maintain them as much active as possible during the trials. The initial higher activity observed during the first day of each trial agrees with the experiment run by Wickins et al. (1996), who found that lobsters spent more time active outside their shelters when they were kept fasting for long periods of time. In the second day (Food), during the first night hours lobsters showed a similar activity pattern compared to the exploration treatment, followed by a decrease a few hours before sunrise. The fidelity to the selected refuge and digestive processes might have negatively affected the activity of lobsters since they had no need to move around in search of food and probably stayed prevalently still for digestion after feeding. Unfortunately, there are no studies reporting the results of experiments on spiny lobsters' diel activity in regards to feeding or other behaviours, so any direct comparison is precluded.

In our study lobsters showed the lowest activity level during the third day of each trial (i.e., Predator). The presence of the octopus in the tank likely induced a cautious behaviour in the lobsters, which stayed still most of the time. The reduced activity due to the perceived danger of predation can have different implications on lobster behaviour. In a predator-rich environment a lower activity could affect feeding and consequently the growing performance or reduce potential mating events, with a negative effect on individual and population growth. The behavioural effect of predators and the anti-predatory responses in crustaceans are well-addressed topics (Barshaw and Spanier, 1994; Bouwma and Herrnkind, 2009; Herrnkind et al., 2001; Ward et al., 2011). Studies on *P. elephas* described a series of anti-predatory behaviours displayed by single specimens and groups of individuals exposed to octopus, which is known to prey on spiny lobsters (Buscaino et al., 2011a; Gristina et al., 2011). These studies focussed on the description of a defence strategy based on sound production (stridulation) and on cooperation among lobsters and were performed in tanks subject to video monitoring (short video-clips recorded only during daylight hours). We can therefore speculate that the higher VariRoll values recorded in presence of the octopus at night were related to an anti-predatory behaviour – possibly stridulation–displayed by the threatened lobster. Indeed, as reported by Zenone et al. (2019), three-axial accelerometers can detect stridulation events in *P. elephas* as a vibration of the carapace, which can well be generated by a lobster hidden inside its shelter.

The description of behaviour and activity of nocturnal, cryptic and aquatic organisms has been a challenge for ethologists and ecologists for decades. The use of accelerometers can contribute to overcome this knowledge gap as their use in monitoring activity (Wang et al., 2015), estimating activity budgets and energy demands (Brownscombe et al., 2017), and quantifying behaviours (Fehlmann et al., 2017; Ladds et al., 2017) in different marine and terrestrial animals has exponentially grown in recent years.

Among lobsters, which are mainly nocturnal and cryptic animals, this technology has been used so far to characterize sound production and energy expenditure (Henninger and Watson, 2005; Lyons et al., 2013; Zenone et al., 2019) or to monitor the activity in *S. latus* (Goldstein et al., 2015). Our study has shed light on the activity pattern of a relatively abundant and commercially important species, even though some limitations deriving from the use of this approach have been highlighted.

As other lobster species, *P. elephas* spends most of the time in a resting state. With the exception of the sudden acceleration associated with sound production or tail flip, the dominant slow movements produce smooth acceleration signals that cannot be adequately described from raw accelerometer data or common derived variables like ODBA and VeDBA, as opposed to what happens with animals with constant movements like for instance a flying bird (Gómez-Laich et al., 2011). The derived variable that we devised allowed us to better represent different levels of activity for *P. elephas* and we deem it could be useful to describe activity patterns and behaviour in other slow-moving species (Wilson et al., 2019) such as sedentary fishes (Beltramino et al., 2019).

5. Conclusions

Accelerometer technology is increasingly being adopted in ecological studies, and the data collected can be successfully used to assess how organisms respond to anthropogenic stressors or to management policies. Accelerometer-based information may improve conservation and management strategies by revealing the detailed responses of individual animals to their surrounding environment, responses such as habitat requirements, effects of predation, behavioural differences among individuals (personality), mating dynamics, trade-off in habitat preferences, changes in activity budget, among others. Moreover, accelerometers can also be used to build ethograms based on a detailed characterization of behaviour and to analyse fine-scale inter-individual dynamics.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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