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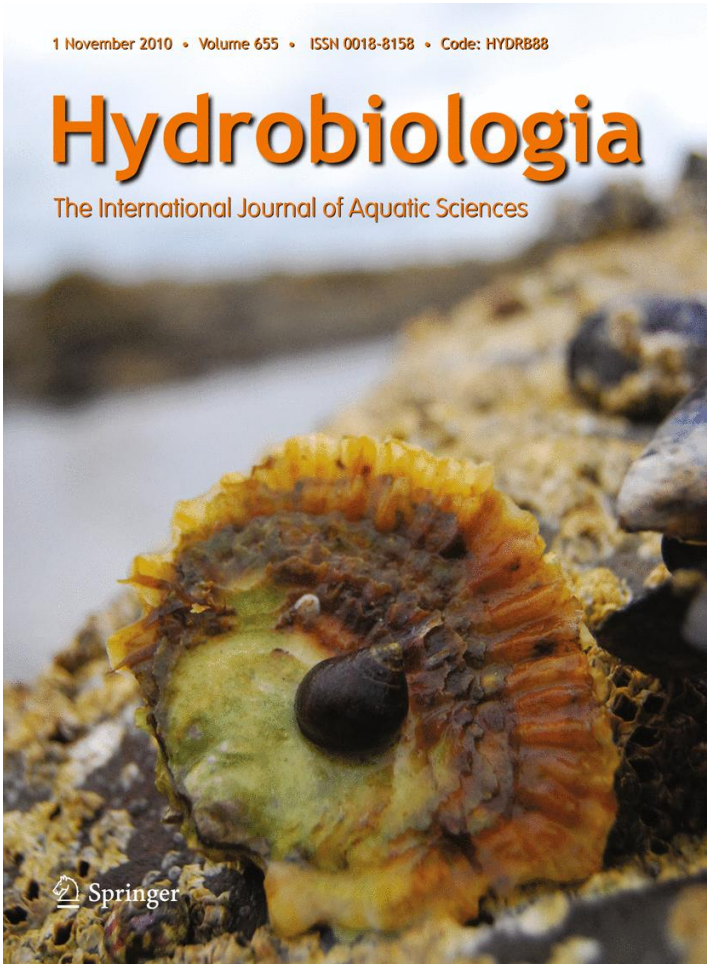
ISSN 0018-8158, Volume 655, Number 1



Hydrobiologia (2010) 655:197–204
DOI 10.1007/s10750-010-0449-7

PRIMARY RESEARCH PAPER

Effect of anthropogenic feeding regimes on activity rhythms of laboratory mussels exposed to natural light

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Received: 22 February 2010 / Revised: 18 August 2010 / Accepted: 23 August 2010 / Published online: 14 September 2010

Abstract Anthropogenic disturbance may affect animal behaviour and should generally be minimised. We examined how anthropogenic disturbance (24 h food deprivation) affected circadian rhythms in laboratory mussels *Mytilus edulis* exposed to natural light in the absence of tides. Repeated measures data were collected on mussel gape angle, exhalant pumping and valve adduction using a Hall sensor system over eight consecutive 24 h periods when exposed to two feeding conditions after 24 h food deprivation. Mussels (fed once per day at either midday or midnight) exposed to natural light showed a clear day–night rhythm with increased nocturnal activity: significantly greater gape angle, increased exhalant pumping and had significantly higher valve adduction rates. However, circadian rhythms were less clear directly after anthropogenic food deprivation, in terms of the circadian rhythm in gape angle becoming significantly more apparent over the following days. Unlike mussels fed at midnight, those fed at midday displayed no significant change in gape angle from the hour before to the hour after they were fed, i.e. mussels given food at midday reacted to this food less than mussels fed at midnight. We suggest that independent of feeding time, laboratory mussels exposed to natural light and free from anthropogenic disturbance increase feeding activity at night because their circadian rhythms are strongly influenced by light levels. This study emphasises that the behaviour of animals in the laboratory and in the wild can be altered by anthropogenic disturbances such as vibrations caused by experimental setups and artificial illumination at night.

Keywords Anthropogenic · Circadian · Tidal · Lunar · Light · Zeitgeber · Bivalve · Behaviour · Rhythm

Handling editor: Pierluigi Viaroli

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Introduction

Mussels are common in intertidal and shallow subtidal areas (Seed, 1976) and are ecologically important as they form large reefs that can enhance local community diversity, providing a critical link between benthic and pelagic systems by filter-feeding

(Seed, 1976; Dame et al., 1991; Beadman et al., 2004). Mussels are robust and readily survive in basic aquariums and, as such, appear to lend themselves to laboratory-based, behavioural studies (see, e.g. Maire et al., 2007). However, despite this apparent advantage, laboratory mussels may behave in a manner different to wild conspecifics if conditions are inappropriate and so may be less useful invertebrate 'laboratory rats' than they seem (Robson, 2008). For example, Rao (1954) demonstrated bimodal lunar-day rhythms of activity in wild mussels when transferred to the laboratory, but Winter (1969) concluded the modifiable rhythmic activity was caused by the artificial laboratory conditions. Winter (1973) found that laboratory mussel activity was not correlated with circadian, or tidal rhythms, which compliments the results of, e.g. Jorgensen (1960), Theede (1963), Davids (1964) and Wilson et al. (2005). However, either day–night or tidal activity rhythms have been reported in subtidal mussels in the wild (e.g. Newell et al., 2005; Wilson et al., 2005; Saurel et al., 2007) and both activity rhythms have been found simultaneously in in situ intertidal mussels during immersion (Robson, 2008).

Blue mussels *Mytilus edulis* have light-sensitive eyes (Morton, 2001) and thus, in the absence of tides, light intensity as a strong Zeitgeber, may have an effect (or have a greater effect) on the rhythmicity of minimally disturbed animals. Indeed, periods of light and dark have been shown to reduce and increase feeding activity and/or growth in blue mussels (Huntsman, 1921; Dodgson, 1928; Coulthard, 1929; Andreu, 1960; Seed, 1969; Strömgren, 1976a, b; Nielsen & Strömgren, 1985; Trevelyan & Chang, 1987). Together with reports of a significant increase in gape angle and number of shell valve adduction events in wild subtidal and intertidal mussels at night (Wilson et al., 2005; Robson, 2008, respectively), it would appear that blue mussels can exhibit higher activity levels during the hours of darkness. In contrast, the constant illumination at night of laboratory mussels may explain why Ameyaw-Akumfi & Naylor (1987) found only a weak tendency for shell-gape to be greatest during the night time. Indeed, periodic or constant illumination at night may explain why neither Newell et al. (2005) nor Saurel et al. (2007) reported greater activity at night, in in situ subtidal mussels. These results raise questions about the ecological variables that affect the activity patterns of mussels and the differences between laboratory and field results (cf. Wilson et al., 2005; Gattermann et al., 2008). Beyond this, the extent and intensity of artificial lighting at night has generally increased around the coasts of developed countries to such an extent that it might have substantial effects on the biology and ecology of species such as mussels in the wild (Longcore & Rich, 2004; Horvath et al., 2009).

In this study, we examine the effect of anthropogenic food deprivation (food deprived for 24 h) on circadian rhythms in laboratory mussels exposed to natural light (a natural Zeitgeber). Mussels were fed once per day, either at midday or at midnight and we hypothesised that mussels given food at midday would initially react less to the addition of food than those mussels fed at midnight. We also hypothesised that mussels would increase their nocturnal activity over time following anthropogenic food deprivation leading to an increasing difference in activity between night and day as time progressed. Data were collected using Hall sensor systems (Wilson et al., 2005; Robson et al., 2007; Robson et al., 2009) to record mussel gape angle, exhalant pumping and valve adduction. Gape angle was used as a proxy for feeding rate (Dolmer, 2000; Wilson et al., 2005; Saurel et al., 2007) although it sometimes corresponds to periods when the mussel foot is actively protruding from the shell. Exhalant pumping was used as a proxy for general activity (Robson et al., 2009). Finally, valve adduction rate was used as a proxy for activities associated with feeding, respiration, and metabolism (Garcia-March et al., 2008).

Materials and methods

All research detailed below was conducted in accordance with institutional, national and international guidelines relating to the use of bivalves in research.

Mussel gape and pumping

Intertidal mussels were collected from LR SS630875 Swansea Bay, Wales, UK at low tide by cutting their byssus threads and transferred to a flow-through aquarium system within 2 h.

Each mussel was subsequently equipped with a Hall sensor system that quantified mussel gape angle (°) with 22 bit resolution (recording gape angle at better than 0.01°) using the methods described by Robson et al. (2009). Equipped mussels were then placed in an aerated flow-through aquarium system containing edible seston-laden seawater from Swansea Bay, Wales, UK for at least a month before being used in experiments. They were subject to natural light conditions, including moonlight from windows and a constant seawater temperature of 14.0°C ± SD 0.4 during non-experimental and experimental periods.

Exhalant mussel pumping (from the top 10 mm of the inhalant siphon and whole of the exhalant siphon) was measured as described by Robson et al. (2009). The mussel and pumping sensor were suspended above the bottom of each tank (Robson et al., 2009), to ensure that the build up of biodeposits on the bottom of the tank during each experiment did not interfere with the mussel or the pumping sensor. No attempt was made to calibrate the high resolution exhalant pumping data. This was due to complications including pseudofaeces strings being eliminated in an exhalant water current out of the top of the inhalant siphon, sometimes when the exhalant siphon was closed; see Robson et al. (2009) for full details and cf. Macdonald et al. (2009). Thus, we display, but do not quantify, the relationship between valve gape and exhalant pumping.

Experiments: feeds at midday and midnight

A sampling frequency of 2 Hz was used to record mussel pumping and gape angle simultaneously (see Ropert-Coudert & Wilson, 2004; Robson et al., 2009). All experiments took place within a 40-day period starting on 26th July 2007. 12 mussels, with an initial mean length of 76.1 ± SD 1.2 mm and mean wet weight of 45.7 ± SD 2.32 g, were placed in separate, gently aerated tanks filled with 12 l of 0.45 μm filtered seawater. They were initially food deprived for 24 h before feeding. All 12 mussels were then fed 300×10^7 *Thalassiosira weissflogii* cells day^{-1} [a concentration of ~250 cells μl^{-1} at one moment in time, which has been associated with both feeding and copious pseudofaeces production (Robson et al., 2010)] at 12 pm (noon) over eight consecutive days (in a first set of experiments). The same 12 mussels were subsequently removed from experimental tanks and kept in an aerated flow-through aquarium system containing edible seston-laden seawater from Swansea Bay, Wales, UK for 2 weeks before then being moved back to experimental tanks and food deprived for 24 h. All mussels were then fed 300×10^7 *Thalassiosira weissflogii* cells day^{-1} at midnight over eight consecutive days (in a second set of experiments). Mussels were fed in a locked laboratory, free from anthropogenic disturbance, using a remote controlled automatic feeder. Hence, the water in the aquaria was not replaced, nor were biodeposits removed. Preliminary mussel ($n = 24$) feeding experiments found cell concentrations in suspension to be minimal 23 h 50 min after each of eight consecutive additions of 300×10^7 *Thalassiosira weissflogii* cells day^{-1}.

Statistical analysis

Gape data was tested for autocorrelation in Minitab 14 (Minitab Inc, State College, PA, USA) and a line delete program (LINEDEL, Jensen Software Systems, Germany) was used to systematically reduce the data set for each mussel when appropriate so that mean gape angle was calculated from non-autocorrelated data. A linear mixed model, including mussel individual as a random factor, was used to examine the difference in gape angle (°) between night and day (night gape minus day gape) of both midday and midnight fed mussels over time after anthropogenic food deprivation. Night was defined as 20:30–05:59:59 and daylight was defined as 06:00:00–20:29:59. Analysis of covariance (ANCOVA) was used to compare the slopes of the two different linear regression lines. Paired *t* tests were used to test for differences in the mean gape angle and adduction rate of mussels in a variety of paired conditions. For data analysis 'valve closure' was defined as gaping <1° (at <1° gape it is not possible to see a visible inhalant/exhalant siphon opening within the two shell valves).

Calculation of the standard error of the estimate from a linear regression

The standard error (σ_0) of an estimate made using a regression equation (SEE) can be used to calculate confidence intervals (CIs) for a regression line (see Zar, 1984, p. 273). However, in the present case, the

inclusion of mussel individual as a random factor leads to the introduction of additional error terms in the calculation of σ_0 (cf. Green et al., 2001):

$$\sigma_0 = \sqrt{\left(\frac{\text{Error}_\text{I}}{n_1}\right) + \left(\frac{\text{Error}_\text{I}}{n_2}\right) + \left(\frac{\text{Error}_\text{S}}{n_3}\right) + \left(\frac{\text{Error}_\text{S}}{n_4}\right) + \left(\left(\text{SE Coef}^2\right) * \left(X_\text{s} - \bar{X}\right)^2\right)}$$

Error_I is the error associated with the variation between individual mussels. Error_S is the error associated with the scatter around the regression line. n_1 is the number of mussels used in each experiment, i.e. included in each regression (=12) and n_4 is the total number of data points associated with those mussels (=96). n_2 is the number of new mussels for which an estimate of mean gape angle is calculated from the regression equation and n_3 is the number of measurements taken from those n_2 new mussels. SE Coef is the standard error of the coefficient. X_s is a predicted value of X (used to predict a value of Y). $\bar{X}$ is the mean of all of the X values used in the original regression. Prediction intervals (i.e. the 'worst case scenario') for the linear regression are calculated by setting both n_2 and n_3 to 1, i.e. the estimate errors (prediction intervals) are calculated as if mean gape angle is estimated from one measurement of mean gape angle from one additional mussel (cf. Green et al., 2009).

Results

Visual inspection of the data for each mussel fed at midday indicated that the first addition of algal cells to mussels which had been food deprived for 24 h induced an increase in valve gape within a few minutes (mean change in the gape angle from the hour before (pre-fed) to the hour after feeding (post-fed): 2.47° ± SE 0.14; $n = 12$ mussels) and a more subtle increase in exhalant pumping. These reached a maximum value in the hours of darkness after the first and subsequent algal additions at midday (e.g. Fig. 1). After the second and subsequent algal additions at midday, mussel response (both gaping and pumping) was less immediate and initially less pronounced (pooled mean change in the gape angle from the hour before to hour after feeding: 0.03° ± SE 0.16, $n = 12$ mussels), with the shell valves sometimes remaining closed for >1 h in daylight after feeding (e.g. Fig. 1). The difference in the change in gape angle from the hour before to the hour after feeding between the first and subsequent feeds at midday was significant ($n = 12$ mussels, $t = 12.01$, $P < 0.001$).

Gape angles and valve adduction rates of mussels fed at midday were significantly greater at night than during daylight ($n = 12$ mussels, mean gape angle during the night and during the day: 4.57° ± SE 0.16 and 3.00 ± 0.14, respectively, $t = 17.36$, $P < 0.001$; mean valve adduction rate during the night and during the day: 4.3 h^{-1} ± SE 0.4 and 1.9 ± 0.3, respectively, $t = 6.44$, $P < 0.001$). The same was true of mussels fed at midnight ($n = 12$ mussels, mean gape angle in night and day: 4.68° ± SE 0.15 and 2.71 ± 0.15, respectively, $t = 31.90$, $P < 0.001$; mean valve adduction rate in night and day: 4.6 h^{-1} ± SE 0.4 and 2.3 ± 0.3, respectively, $t = 4.56$, $P = 0.001$). Circadian rhythms became significantly more apparent, in terms of the difference in gape angle between night and day, in fed mussels

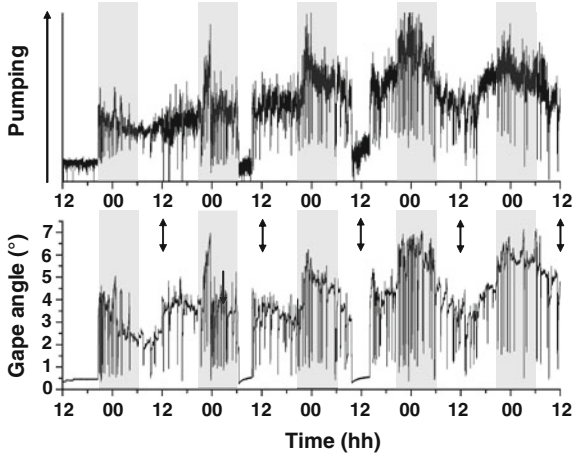

Fig. 1 Example of the gape angle and exhalant pumping of a 77-mm long blue mussel *Mytilus edulis* over 24 h food deprivation followed by four consecutive days when fed 300×10^7 *Thalassiosira weissflogii* cells day^{-1} at midday (12 pm). *Shaded areas* indicate approximate periods of darkness. *Double headed arrows* indicate time fed

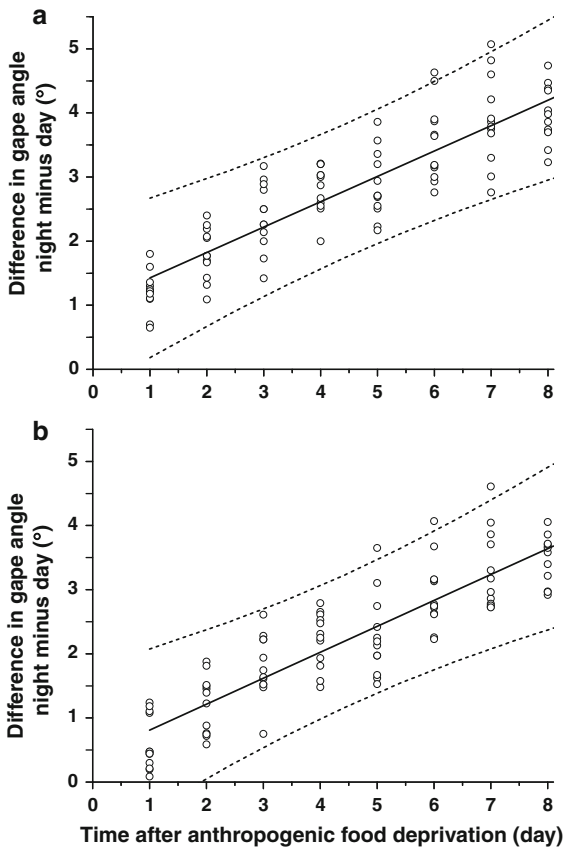

Fig. 2 The difference in gape angle between night and day (night gape minus day gape) of fed blue mussels *Mytilus edulis* ($n = 12$) over time after anthropogenic food deprivation **a** fed at midday ($y = 0.396x + 1.030$; $R^2 = 0.85$, $P < 0.001$), **b** fed at midnight ($y = 0.405x + 0.403$; $R^2 = 0.83$, $P < 0.001$). The best-fit regression line (*solid line*) and 95% prediction intervals (*broken lines*) are included (see 'Calculation of the standard error of the estimate from a linear regression' section)

over time after anthropogenic food deprivation (e.g. Fig. 1). This was quantified by a linear mixed model (including mussel individual as a random factor) relating the difference in mean gape between night and day over time after anthropogenic food deprivation (Fig. 2: fed midday: $F_{1,83} = 415.09$, $P < 0.001$, fed midnight: $F_{1,83} = 371.98$, $P < 0.001$). The slopes of the two different (fed midday and fed midnight) linear regression lines were not significantly different ($F_{1,177} = 0.09$, $P = 0.758$, overall slope = 0.400).

Mussels fed at midnight gaped significantly less during the hours of darkness before midnight than was the case for mussels fed at midday ($n = 12$ mussels per condition, mean gape angle during the hours of darkness before midnight: 3.20° ± SE 0.12 and 4.60 ± 0.12, respectively, $t = 29.06$, $P < 0.001$, Fig. 3). The time at which mussels were fed influenced the extent of the change in gape angle and pumping between the pre-fed and post-fed states (Fig. 3). For mussels fed at midday overall there was no significant change in the gape angle from the hour before (pre-fed) to the hour after they were fed (post-fed) ($n = 12$ mussels, mean gape angle before and after feeding 2.51° ± SE 0.12 and 2.56° ± 0.10, respectively, $t = 0.37$, $P = 0.72$). However, for mussels fed at midnight (in darkness), there was a significant increase in gape angle from the hour before to the hour after they were fed. The mean gape angle increased from 3.61° ± SE 0.11 to 6.22° ± 0.30 ($n = 12$ mussels, $t = 7.82$, $P < 0.001$). Mussel activity was not correlated with lunar or tidal rhythms.

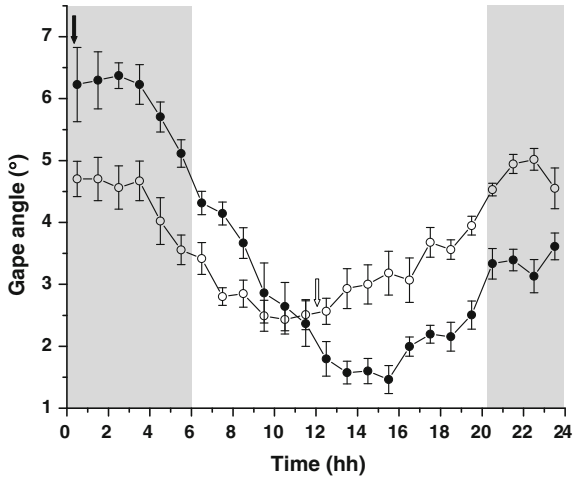

Fig. 3 Mean blue mussel *Mytilus edulis* gape angle over time. Mussels ($n = 12$) were fed 300×10^7 *Thalassiosira weissflogii* cells day^{-1} over eight consecutive days at either midday (*clear arrow*) or midnight (*black arrow*). *Clear* and *black circles* indicate mean gape ± SE of mussels fed at midday and midnight, respectively. *Shaded areas* indicate approximate periods of darkness

Discussion

Daily activity rhythms are nearly universal among animals and their specific patterns are adaptations for appropriate habitat exploitation (for example, see Clarke, 1978; Wilson et al., 1993; Hays, 2003). Our results show that blue mussels in the laboratory exposed to natural light are significantly more active

at night (e.g. Figs. 1, 3) and as we hypothesised their nocturnal activity increased over time after anthropogenic food deprivation (Fig. 2). This implies that both anthropogenic disturbance and light regime affect the circadian activity patterns of blue mussels (cf. Wilson et al., 2005), the latter factor from artificial lights shining on wild mussels in coastal waters at night (cf. Newell et al., 2005; Saurel et al., 2007) may well alter their natural rhythms (cf. Longcore & Rich, 2004; Horvath et al., 2009).

In the current study, the day–night rhythm of the mussels, where greater activity is exhibited during darkness, was affected by the unnatural feeding conditions (cf. Higgins, 1980; Williams & Pilditch, 1997). For example, mussels had low gape angles, pumping activity and valve adduction rate when they were food deprived for 24 h, especially during daylight, and responded by increasing these measures of activity when fed (e.g. Fig. 1). After food deprivation, only after the first addition of food, was there a significant increase in the activity of the mussels when being fed at midday. This suggests that their need for nutrients at this point, at least to some degree, overrode their circadian rhythm; a demonstration of behavioural plasticity in response to a strong requirement to feed. Beyond the first day of feeding, day-fed mussels showed no significant increase in activity in the hour after the addition of food and were most active at night. Thus, as we hypothesised, mussels fed at midday generally reacted less to the addition of food compared to the significant reaction of mussels fed at midnight, indicating the strong effect of the circadian rhythm, likely influenced by light levels. Feeding mussels at midnight significantly suppressed their gape angle during the hours of darkness before midnight compared to mussels fed at midday (Fig. 3), which is likely due either to conditional learning to midnight feeding or because by the late hours of the day food in the water is negligible and thus feeding activity is not productive.

The adaptive significance of high nocturnal activity in mussels is unclear. One possibility is that such day–night gaping patterns are part of a strategy to feed while minimising the likelihood of predation by visually feeding predators (Ameyaw-Akumfi & Naylor, 1987). For example, Oystercatchers *Haematopus ostralegus*, feed, in part, on gaping immersed and emersed mussels (e.g. Norton-Griffiths, 1967; Sutherland & Ens, 1987; Goss-Custard, 1996; Stillman et al., 2000). However, some visually feeding predators such as eider ducks *Somateria* spp. predate on mussels regardless of whether they are gaping or not. Another, related possibility is that such day–night gaping behaviour may depend on the circadian rhythm reported for blue mussels relating to byssus thread production, where there is greater thread production during the night (Martella, 1974). From our observations, we suggest that mussels may be particularly vulnerable to predation when the foot (used as a plantar during attachment of the byssus to the substrate) is protruding from the shell because when handled, mussels adduct their valves around their foot and thus cannot fully adduct their valves.

In conclusion, our data suggest that laboratory mussels exposed to natural light, and free from anthropogenic disturbance (such as vibrations caused by experimental setups) increase their feeding activity at night, even when repeatedly fed during the day, because their circadian rhythms are strongly influenced by light levels. However, clearly light is not the only factor influencing the activity levels of mussels, which demonstrate an ability to adjust their activity patterns in response to the timing of food availability. Future work researching the natural rhythms of species should aim for the provision of natural light regimes (e.g. research on minimally disturbed animals in the wild) and for data to be obtained that allows determination of when the effects of anthropogenic factors are negligible. When working with mussels in a laboratory context, we suggest that analysis of activity rhythms should be undertaken on data collected from at least a week after anthropogenic disturbance. However, since anthropogenic illumination at night alters natural light regimes in terrestrial and aquatic ecosystems around the world (Longcore & Rich, 2004), exposing species to natural conditions may be difficult, especially in urban areas.

Acknowledgments We are most grateful to Jonathan Green, Graeme Hays, Martin Lilley and James Wilson for help during the study. This work was funded by the European Social Fund and Deep Dock Ltd.

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