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## SHORT COMMUNICATION

# The contraction–expansion behaviour in the demosponge *Tethya wilhelma* is light controlled and follows a diurnal rhythm

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## ABSTRACT

Sponges (phylum Porifera) are metazoans which lack muscles and nerve cells, yet perform coordinated behaviours such as whole-body contractions. Previous studies indicate diurnal variability in both the number of contractions and the expression of circadian clock genes. Here, we show that diurnal patterns are present in the contraction–expansion behaviour of the demosponge *Tethya wilhelma*, by using infrared videography and a simulated night/day cycle including sunrise and sunset mimics. In addition, we show that this behaviour is at least strongly influenced by ambient light intensity and therefore indicates light-sensing capabilities in this sponge species. This is supported by our finding that *T. wilhelma* consistently contracts at sunrise, and that this pattern disappears both when the sponge is kept in constant darkness and when it is in constant light.

**KEY WORDS:** Porifera, Pre-nervous system, Light reception, Behavioural control, Diurnal rhythmicity

## INTRODUCTION

Sponges (phylum Porifera) are aquatic animals with a global distribution, found at all water depths. The group comprises over 9500 accepted species across four extant classes, of which class Demospongiae is the most diverse (<http://www.marinespecies.org/porifera> accessed 3 November 2022; Van Soest et al., 2012). The sponge body is organized around a complex system of cavities and canals allowing water to flow through the sponge (Asadzadeh et al., 2020). Sponges possess a number of different cell types, but lack muscle and nerve cells (Lavrov and Kosevich, 2014; Musser et al., 2021); however, they can perform coordinated behaviours such as whole-body contractions, and some even have the ability to move (Bond, 2013; Nickel, 2006). These contractions occur spontaneously, but can also be initiated by a range of different chemical stimuli (Elliott and Leys, 2010; Ellwanger et al., 2007; Ellwanger and Nickel, 2006; Goldstein et al., 2020) and mechanical stimuli locally applied to the exopinacoderm, which result in a contraction wave spreading across the surface of the sponge (Elliott and Leys, 2007; Nickel et al., 2011). This is seen in the freshwater sponge *Ephydatia muelleri* where both shaking and exposure to high loads of ink particles lead to a contraction, the latter resulting in the expulsion of waste particles from its water canal system (Elliott and Leys, 2007). The mechanism initiating this behaviour is unknown, although primary cilia located in


the oscular area are suggested to function as mechanoreceptors involved in water flow regulation and sponge body contractions (Ludeman et al., 2014). Despite the lack of nerve cells, stimulation of one part of the sponge often results in behavioural changes throughout the entire sponge, suggesting coordination which is possibly facilitated by chemical messengers (Kealy et al., 2019). Light also influences sponge behaviours such as the release of larvae, which in some species is correlated with the lunar cycle (Amano, 1986, 1988; Hoppe and Reichert, 1987; Neely and Butler, 2020). Likewise, some sponge larvae respond to changes in light conditions, suggesting that they possess a light-sensory system (Leys et al., 2002). However, genetic data suggest that sponges lack the photopigment opsin, most often involved in animal light reception, and larval studies of the demosponge *Amphimedon queenslandica* indicate that this function is fulfilled by cryptochromes instead (Mah and Leys, 2017; Rivera et al., 2012). In addition to performing behaviours normally associated with a nervous system, sponges also possess many of the genes associated with the nervous system in other animals. This has led to the hypothesis that sponges, while not having a nervous system per se, either possess nerve-like elements resembling a pre-nervous system or possess remnants of a nervous system, able to perform some of the functions normally only seen in proper nerve cells (Leys, 2015; Musser et al., 2021).

Diurnal rhythms are observed in many different types of organisms. In animals, a typical pattern consists of alternating periods of inactivity, i.e. sleep, and an active phase (Siegel, 2008). These patterns also occur in animals without a conventional brain (for a definition, see Richter et al., 2010) such as the cnidarian polyp *Hydra vulgaris* (Kanaya et al., 2020) and the jellyfish *Cassiopea* sp. (Nath et al., 2017). However, studies of diurnal rhythms in animals without nerve cells are very limited. In a long-term *in situ* study, Reiswig (1971) showed a synchronized diurnal cycle of body contractions and expansions of the demosponge *Tectitethya crypta*. Another demosponge, *Tethya wilhelma*, also seems to exhibit diurnal variation in body contractions, as indicated by two specimens tested under laboratory conditions with an artificial 12 h:12 h light:dark cycle (Nickel, 2004). The control mechanisms behind the diurnal rhythm were not tested; however, molecular work on *A. queenslandica* revealed a diurnal cycle in the expression of two metazoan circadian clock genes, suggesting that it could be at least partly intrinsically regulated (Jindrich et al., 2017). The detection of diurnal rhythms appears to differ between species and possibly also experimental conditions; for example, an *in situ* study on the demosponge *Aplysina aerophoba* did not suggest any diurnal rhythms to pumping activity (Pfannkuchen et al., 2009), whereas an *ex situ* study on the sponge *Cliona orientalis* indicated diurnal periodicity in both pumping rates and oscula contractions (Strehlow et al., 2016).

In this study, we assessed the diurnal rhythm in the body contraction–expansion of the sponge *T. wilhelma* indicated from previous studies, and tested the potential influence of ambient light

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intensity by manipulation of the light regime. We confirmed the presence of diurnal rhythms in the contractions, and also found evidence for the rhythm to, at least largely, be controlled by ambient light levels.

## MATERIALS AND METHODS

### Culturing of sponges

Specimens of *Tethya wilhelma* Sarà, Sarà, Nickel & Brümmer, 2001 were collected at the National Aquarium of Denmark, the Blue Planet (Copenhagen, Denmark), in a coral reef display tank with seawater of 24°C and 33 psu. The specimens had a diameter of 0.5–1.0 cm. They were transported to Aarhus University where they were transferred to individual wells of a six-well culture plate. Each well had a 2.5 cm diameter black plastic disc placed at the bottom for attachment. The well plate was then placed in a 25 l glass tank with seawater collected near Lemvig, Denmark, adjusted to 32–34 psu using artificial Instant Ocean sea salt (Aquarium Systems, Sarrebourg, Lorraine, France). The water temperature was kept at 22°C, controlled by the room temperature. The tank water was filtered and circulated using an EHEIM eXperience 150 external filter pump, which included a biological filter (EHEIM GmbH & Co. KG, Deizisau, Germany). Light was supplied by a Fluval Plant Nano Bluetooth LED light (Rolf C. Hagen Inc., Baie d'Urfé, QC, Canada), programmed to simulate sunrise with a linear increase in light intensity from 06:00 h to 07:00 h, daylight from 07:00 h to 17:00 h, sunset with a linear decrease in light intensity from 17:00 h to 18:00 h, and dark from 18:00 h to 06:00 h. The light intensity and emission profile were measured with a RAMSES radiometer (TriOS Mess- und Datentechnik GmbH, Rastede, Germany) (Fig. S1A). During the daytime, the light had an intensity of  $0.8 \times 10^{17}$  photons  $m^{-2} s^{-1}$ , corresponding to normal room light intensity. Approximately one-third of the water in the tank was exchanged every 3 weeks throughout the experimental period.

### Experimental setup

The sponges were transferred to a submerged clear acrylic box (12×17×4.8 cm, H×W×D) inside the holding tank. Light could enter directly from above and from the sides, except the back which was covered with black fabric to provide a uniform dark background for video recordings. A weight was placed on top of the box to prevent it from moving as a result of the water currents in the tank during video recordings. The sponges were filmed from the outside of the tank to document changes in the sponge body volume, measured as changes in the projected area. Recordings were made with a Panasonic HC-VX980 digital camcorder (Panasonic Corp.) using the night mode setting. Two infrared LED light sources (peak emission at 940 nm) were used for illumination during the night (Fig. S1B,C).

### Test for diurnal rhythm

To characterize the contraction pattern of *T. wilhelma* under simulated natural dark/light conditions, six specimens were filmed one at a time for 72 h each. The sponge to be filmed was transferred to the recording chamber at least 3 h before the start of the recording session to minimize the influence of handling. All recordings began at 18:00 h on the first day and after 72 h of recordings, the sponge was transferred back into the well plate. The influence of the light regime on contraction cycles was investigated by subjecting six new specimens to 72 h of constant light and 72 h of constant dark. These two treatments were separated by a 7 day recovery period with a 12 h:12 h dark:light cycle. During the recovery period, the sponges were placed in another tank. Three sponges were tested at the same

time and they were again transferred to the recording chamber at least 3 h before the start of the experiment. Because the experimental period started at 18:00 h, a simulated sunset was included at the onset of the constant darkness experiments but not the constant light experiment. To ensure complete control of the light environment in the experimental tank, the tank was covered by a light proof box also including the camera and light sources.

### Processing of video material

Single frames were extracted from the videos with a time resolution of 100 s and transferred to the software program ImageJ (Rasband, 2020) as an image stack. Here, a scale bar was added using the plate the sponges were attached to as a reference. The images were converted into 8-bit greyscale, cropped, and the brightness and contrast adjusted to optimize the contrast between sponge and background. Because of the contrast between the bright sponge and the dark background, the part of the image containing the sponge could be selected by converting the image to a binary image by setting an appropriate threshold and applying it to the image stack. The projected area of the sponge was then measured using the 'Measure Stack' macro in ImageJ (Fig. S1D).

### Analysis of contraction patterns

The area measurements of each sponge were normalized by the maximum area during the 72 h period to obtain a relative projected area (RPA) (see Goldstein et al., 2020). The mean RPA for each 12 h period (06:00 h to 18:00 h and 18:00 h to 06:00 h) was calculated with a time resolution of 100 s. The number of fully contracted states, identified as RPA minima, was also counted for each 12 h time period. The mean contraction amplitude was calculated for each 12 h time period as the mean change in RPA between the initiation of the contractions and the fully contracted states during that time period. The mean contraction area was calculated as the mean RPA of the fully contracted states during each 12 h period. Lastly, the minimum and maximum RPA during each 12 h time period were identified. If a contraction spanned both dark and light periods, then it was assigned to the period where the contraction was initiated. The sponges are constantly making small changes of their volume and accordingly a 7% reduction in RPA was set as the threshold before it was considered a contraction. This threshold was chosen as contractions exceeding a 7% reduction in RPA displayed the typical shape of a contraction, with a relatively fast contraction, followed by a slower expansion phase. Summarized contraction–expansion graphs were produced for each of the three experiments by combining the individual specimens ( $N=5$  or 6) and the individual days ( $N=3$ ) into one graph to reveal possible consistent patterns in the timing of the individual contractions within the 24 h light cycle. Here, 95% confidence intervals were reported.

### Statistical analyses

The statistical analyses were performed in RStudio version 2022.02.1 (<https://posit.co/>), using the R packages 'lme4' (Bates et al., 2015) and 'lmerTest' (Kuznetsova et al., 2017). Plots were made using the package 'ggplot2' (Wickham, 2016) and Microsoft Excel. Linear mixed-effect models (LMEMs) were fitted, which met the assumptions of normal distribution, homoscedasticity and independence of residuals. Response variables used were: mean RPA, mean relative contraction amplitude, mean RPA of contractions, minimum RPA and maximum RPA. Explanatory variables were included as follows: day period (either day or night) was added as a fixed factor, and sponge ID and day number were added as random effects. For the analysis of the number of fully

contracted states, a generalized linear mixed model (GLMM) with Poisson distribution was fitted to the data. This model met the same assumptions and contained the same explanatory variables and random effects as the LMEMs. In the comparisons between experiments (dark/light, constant dark and constant light), experiment was added as a fixed factor instead of period, and *post hoc* tests were performed by multiple comparisons of means using Tukey contrasts and single-step method for adjusting *P*-values using the 'glht' function from the R package 'multcomp' (Hothorn et al., 2008). The critical *P*-value was set to 0.05 for all tests. Standard deviations ( $\pm$ s.d.) were calculated based on the number of specimens with the experimental days pooled together.

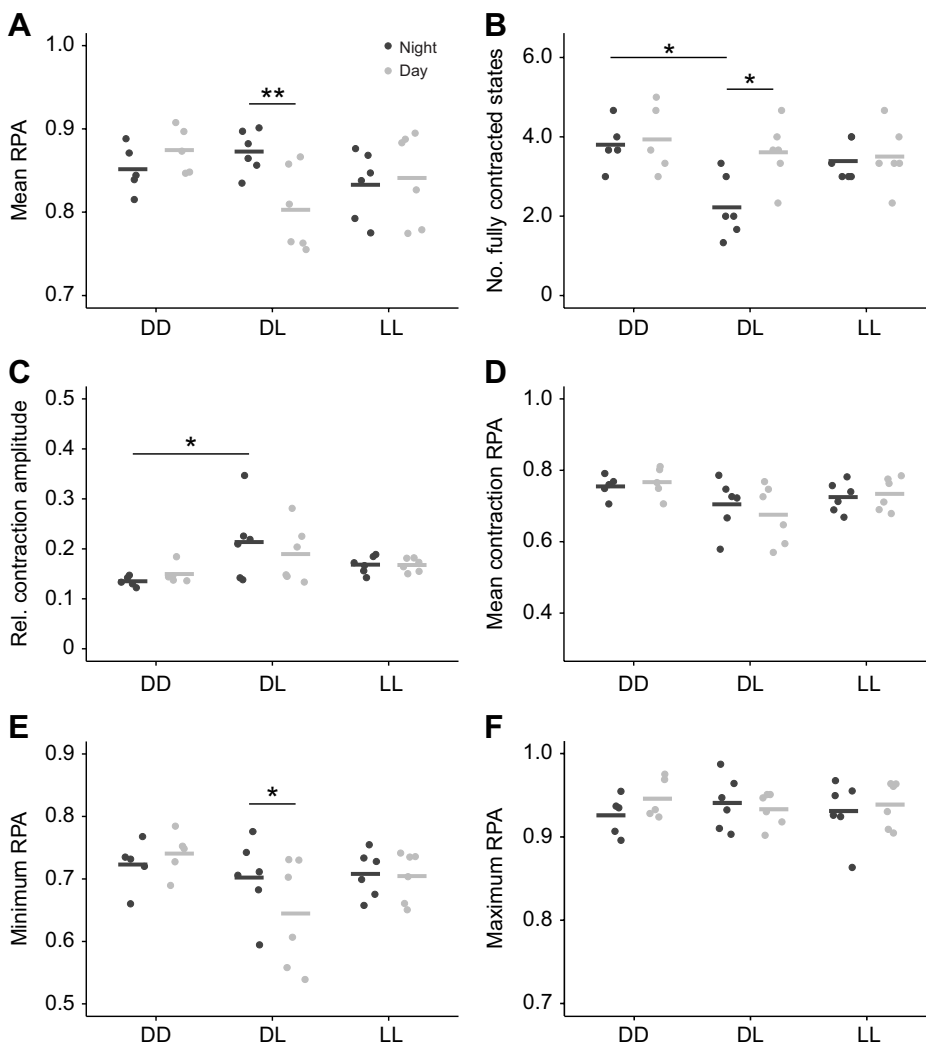
## RESULTS AND DISCUSSION

### Diurnal rhythms

When sponges were kept under normal light conditions ( $N=6$ ), the mean ( $\pm$ s.d.) RPA was  $0.873\pm 0.026$  for the night periods and  $0.803\pm 0.050$  for the day periods, which is a significant difference (LMEM,  $t=3.6$ ,  $P=0.001$ ) (Fig. 1A). The mean number of fully contracted states also differed significantly between night and day periods (GLMM,  $z=-2.4$ ,  $P=0.016$ ) with a mean ( $\pm$ s.d.) of  $2.22\pm 0.78$  during night periods and  $3.61\pm 0.77$  during day periods (Fig. 1B). The mean relative contraction amplitude was  $0.214\pm 0.076$  during the night and  $0.190\pm 0.058$  during the day (Fig. 1C). This difference was not significant (LMEM,  $t=1.2$ ,  $P=0.239$ ) and

neither was the difference in the mean contraction RPA, which was  $0.705\pm 0.073$  and  $0.676\pm 0.083$  for night periods and day periods, respectively (LMEM,  $t=1.5$ ,  $P=0.135$ ) (Fig. 1D). The mean minimum RPA was  $0.702\pm 0.062$  during the night period and  $0.645\pm 0.087$  during the day period, and this difference was significant (LMEM,  $t=2.3$ ,  $P=0.028$ ) (Fig. 1E). Finally, the maximum RPA did not differ between the night period,  $0.941\pm 0.032$ , and the day period,  $0.933\pm 0.020$  (LMEM,  $t=0.4$ ,  $P=0.684$ ) (Fig. 1F).

The present study shows a diurnal rhythm in the contraction patterns of *T. wilhelma*, whereby the body is more expanded during the night and more actively contracted diurnally. These findings support another study on this species by Nickel (2004), where projected area measurements were also used to compare the number of contractions during day and night. However, the study by Nickel (2004) was limited to two specimens; therefore, the present study is the first to statistically prove this diurnal rhythm occurs in *T. wilhelma*. In addition, our results show that this diurnal rhythm is not restricted to the number of contractions alone but is also present in two additional parameters: minimum and mean relative projected area. Nevertheless, it should be noted that these three parameters are not completely independent, as more contractions equal more minima, and more time spent in a contracted state leads to lower mean RPA. For functional considerations of the contractions in sponges, it is important to note that although



**Fig. 1. Influence of light regime on contraction–expansion behaviour of *Tethya wilhelma*.** Differences between experiments (DD, constant dark; DL, dark/light; and LL, constant light), and between night period (dark grey) and light period (light grey) in mean relative projected area (RPA) (A), number of fully contracted states (B), mean relative contraction amplitude (C), mean contraction RPA (D), minimum RPA (E) and maximum RPA (F). Asterisks indicate a significant difference: \* $P < 0.05$ , \*\* $P < 0.01$ . Points are individual specimens ( $N=5$  for DD,  $N=6$  for DL and LL); bars are means.



**Table 1. Results from dark/light, constant dark and constant light experiments in *Tethya wilhelma***

Experiment	Night period	Day period	<i>t</i> (z)	<i>P</i>
Simulated dark/light experiment				
Mean RPA	0.873±0.026	0.803±0.050	3.6	0.001
No. fully contracted states	2.22±0.78	3.61±0.77	-2.4	0.016
Mean relative contraction amplitude	0.214±0.076	0.190±0.058	1.2	0.239
Mean contraction RPA	0.705±0.073	0.676±0.083	1.5	0.135
Minimum RPA	0.702±0.062	0.645±0.087	2.3	0.028
Maximum RPA	0.941±0.032	0.933±0.020	0.4	0.684
Constant darkness experiment				
Mean RPA	0.852±0.029	0.875±0.028	-1.5	0.155
No. fully contracted states	3.80±0.61	3.93±0.86	-0.2	0.853
Mean relative contraction amplitude	0.135±0.010	0.150±0.020	-1.0	0.314
Mean contraction RPA	0.755±0.032	0.767±0.042	-1.0	0.350
Minimum RPA	0.723±0.039	0.748±0.035	-1.6	0.131
Maximum RPA	0.926±0.024	0.946±0.024	-1.1	0.280
Constant light experiment				
Mean RPA	0.833±0.041	0.841±0.055	-0.5	0.652
No. fully contracted states	3.39±0.49	3.50±0.78	-0.2	0.857
Mean relative contraction amplitude	0.168±0.017	0.168±0.013	0.0	0.977
Mean contraction RPA	0.725±0.043	0.734±0.046	-0.7	0.485
Minimum RPA	0.708±0.037	0.705±0.040	0.3	0.746
Maximum RPA	0.931±0.037	0.939±0.028	-0.4	0.668

Mean (±s.d.) values for each of the six examined parameters during the night periods and the day periods. For comparisons between periods, *t*- and *P*-values are presented, except for no. fully contracted states, where *z*- and *P*-values are presented.

contractions result in changes of the overall volume of the sponge, these changes mainly concern the volume of the water canal system (Nickel et al., 2011). Sponge contractions have been suggested to serve different functions, including as a cleaning mechanism to expel unwanted particles by flushing the water canal system (Elliott and Leys, 2007; Nickel, 2004). In this case, diurnal periodicity in contraction–expansion behaviour could be related to maintenance of the water canal system. Further studies are needed to explore the relationship between diurnal rhythms in activity patterns and individual elements of the water canal system, and to test the hypothesis that *T. wilhelma* is more actively filtering during the daytime and thus needs more flushing in this period.

### Influence of light environment

Under constant darkness ( $N=5$ ) and constant light conditions ( $N=6$ ), no significant differences were found between night and day periods in any of the six examined parameters (Table 1, Fig. 1). When comparing the actual daytime between the experiments, the mean RPA was significantly higher in the constant dark experiment compared with the dark/light experiment according to the LMEM ( $t=-2.3$ ,  $P=0.040$ ), but in the multiple comparisons test this trend was not significant (Tukey comparisons *post hoc*:  $P=0.054$ ) (Fig. 1A). Also, minimum RPA was significantly higher in the constant dark experiment compared with the dark/light experiment according to the LMEM ( $t=-2.3$ ,  $P=0.047$ ), but again this trend was not significant according to the multiple comparisons test (Tukey comparisons *post hoc*:  $P=0.055$ ) (Fig. 1E). The constant light experiments did not differ significantly from the two other experiments for any of the six parameters (Fig. 1). When comparing the actual night-time between the three experiments, the number of fully contracted states was significantly higher in the constant dark experiment compared with the dark/light experiment

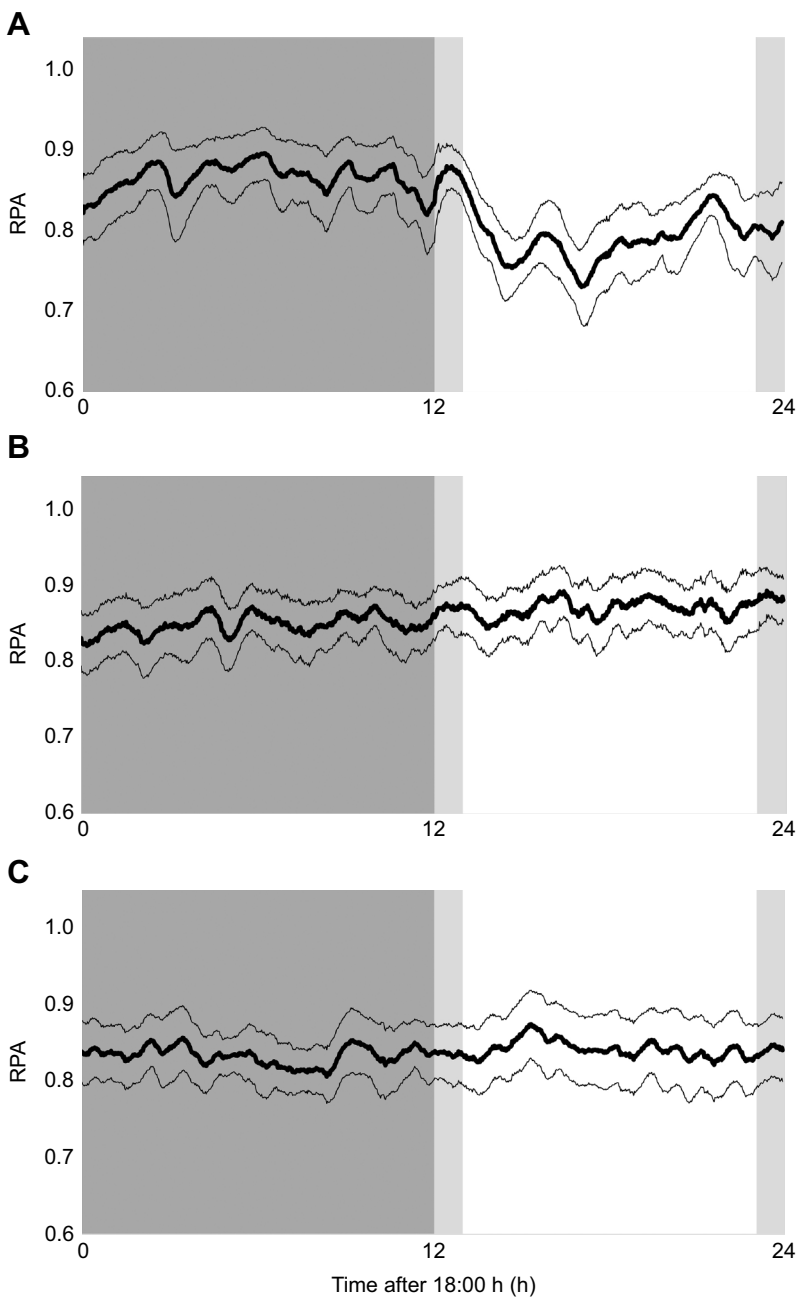
(Tukey comparisons *post hoc*:  $P=0.025$ ) (Fig. 1B), and the mean relative contraction amplitude was significantly lower in the constant dark experiment compared with the dark/light experiment (Tukey comparisons *post hoc*:  $P=0.028$ ) (Fig. 1C). Again, the constant light experiment did not differ significantly from the two other experiments for any of the parameters (Fig. 1).

Furthermore, the summarized contraction–expansion diagrams showed a consistent pattern of one contraction happening shortly after the time of sunrise in the simulated dark/light experiment (Fig. 2A; Fig. S2). This pattern was observed in neither the constant dark nor the constant light experiments (Fig. 2B,C; Fig. S3A,B).

Our study shows the absence of diurnal rhythms in *T. wilhelma* under constant dark and constant light conditions, implying that contraction behaviour is, at least in part, regulated directly by ambient light intensity. These results suggest that this sponge has light-sensing capabilities. This is supported by our finding that a contraction occurs shortly after simulated sunrise, which may indicate that sunrise serves as a cue of when to increase activity, i.e. contractions, potentially flushing the canal system prior to increased daytime filtration. Such light sensing might have influenced the previously mentioned study by Nickel (2004), wherein an external flash was used to capture images of the contraction states of *T. wilhelma*. Further studies are needed to determine a possible behavioural impact of exposure to short flashes of light during the night and clarify whether this could influence the natural contraction patterns, such as by initiating a contraction similar to those observed at sunrise. In our study, filming was conducted under infrared light, removing the potential problem. Also, our inclusion of a simulated sunrise and sunset in the light cycle results in more natural changes of light levels. This may explain why the contraction initiated by sunrise suggested in our results was not reported by Nickel (2004), who did not include a sunrise and sunset phase in the 12 h:12 h light:dark cycle.

Interestingly, we found that under constant darkness the animals did not display the night-time behaviour of the animals in dark/light experiments. Under constant darkness, the number of fully contracted states and the mean relative amplitude of the contractions were similar to those of normal daytime behaviour. We have no clear indications of why this is so, but it could indicate a high level of stress during unnatural light conditions. It should be noted that the multiple comparisons *post hoc* tests failed to show differences among experiments in mean RPA and minimum RPA during the timewise day periods. This is probably due to low statistical power caused by unequal sample sizes between experiments, and as the differences in means show, effects sizes are clearly large and confirm that the sponges are more expanded during darkness than during light (Fig. 1A,E).

The diurnal rhythm in *T. wilhelma* supports genomic studies on another demosponge *A. queenslandica*. Here, diurnal variations were found in the expression of two circadian clock genes, but the variations became less pronounced when the sponge was subjected to constant darkness (Jindrich et al., 2017). This suggests at least some endogenous control of diurnal rhythms acting alongside the light control shown by our results. Many sponge species have a diverse microbiome, which includes photosynthesizing symbionts (Bickmeyer et al., 2019; Thomas et al., 2016). The diurnal rhythm of the sponge could be influenced by this microbiome, as the associated decrease in oxygen levels inside the sponge at night could account for such behavioural changes. However, this is contradicted by the very similar patterns observed under constant darkness and constant light. As the sister group to Bilateria, cnidarians are amongst the simplest animals with neurons; here,



**Fig. 2. Summarized contraction–expansion graphs of specimens of *T. wilhelma*.** Mean RPA over 3 days for all specimens are shown with thick lines and 95% confidence interval with thin lines. (A) Simulated night/day cycle ( $N=6$ ), (B) constant dark ( $N=5$ ) and (C) constant light ( $N=6$ ). Dark grey indicates night period, light grey indicates periods with sunrise/sunset.

light seems to play a similar role in their diurnal rhythms to that which we found in *T. wilhelma*. Studies of *Hydra vulgaris*, *Tripedalia cystophora* and *Copula sivickisi* all show behaviours with diurnal rhythms directly influenced by ambient light intensity (Garm et al., 2012; Kanaya et al., 2020). Changes in behaviour in response to light are also observed among the sister group to animals, the choanoflagellates. For example, Brunet et al. (2019) revealed that colonies of the choanoflagellate *Choanoeca flexa* inverted when subjected to changing light levels, showing that even simple holozoans can modulate their behaviour in response to light. This suggests that such behaviour in sponges is not at all unexpected.

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#### Competing interests

The authors declare no competing or financial interests.

#### Author contributions

Conceptualization: S.B.F., A.G., P.F.; Methodology: S.B.F., A.G., P.F.; Formal analysis: S.B.F.; Investigation: S.B.F.; Resources: A.G., P.F.; Writing - original draft: S.B.F.; Writing - review & editing: S.B.F., A.G., P.F.; Visualization: S.B.F.; Supervision: A.G., P.F.; Funding acquisition: A.G., P.F.

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## Data availability

All relevant data can be found within the article and its supplementary information.

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