Turning the tide: Rhythmic aggregation behaviour in *Anurida maritima* (Collembola) is entrained by inundation

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ABSTRACT

Numerous foreshore species evolved the ability to predict tidal change and adjust behaviour and metabolism accordingly. The intertidal collembolan *Anurida maritima* (Guérin-Méneville, 1836) shows endogenously controlled rhythmic changes in behaviour that anticipate the tides. Animals forage during low tide and hide in large aggregations in the substrate during high tide. Here, artificial tidal environments and time-lapse photography were used to investigate if this behaviour is responsive to key environmental cues. It is shown that the precise rhythmicity of aggregation behaviour is dependent on periodic inundations. In the absence of such inundations, rhythmic aggregation patterns dissipate and are no longer accurate after 14 days. Slowly shifting the artificial tides, showed that rhythmic aggregation behaviour in *A. maritima* is responsive and adjusts to a newly-imposed tidal regimen. This suggests that the species has the ability to synchronise to newly encountered tidal conditions under natural conditions. The findings provide a robust foundation for advancing detailed chronobiological research on *A. maritima* as a model organism to gain a deeper understanding of biological time-keeping.

1. Introduction

Most living organisms are exposed to predictable recurring environmental changes, such as those caused by Earth's rotation on its axis relative to the Sun. The predictability of these fluctuations has resulted in the evolution of endogenous clock-like mechanisms that allow organisms to anticipate upcoming change and adjust their physiology, metabolism, or behaviour accordingly (Paranjpe and Sharma, 2005; Patke et al., 2020). The best studied biological oscillations are circadian rhythms that are tuned to the day-night cycle. Other biological oscillations exist, but these have received far less scientific interest (Kaiser and Neumann, 2021). They include biological rhythms aligned to predictable rises and falls in sea levels (i.e. tides) that are affected by the Moon's relative position to Earth (Häfker et al., 2023). Such circatidal rhythms have been reported for organisms that live in the intertidal zone, i.e. the area that is exposed at low tide and submerged at high tide (Rock et al., 2022). Environmental conditions within the intertidal zone are harsh and show extreme variation, shifting between marine and terrestrial environments twice within each tidal day of approximately 24 h and 50 min. Hence, within the foreshore environment an ability to correctly predict upcoming change is of major importance, as not being able to do so could be fatal.

Within the intertidal zone some species are active when the area is submerged (e.g. *Eurydice pulchra* (Isopoda) (Hastings and Naylor, 1980) and *Parhyale hawaiensis* (Amphipoda) (Kwiatkowski et al., 2023)), whilst other species are active when the area is dry (e.g. *Callytron inspecularis* (Coleoptera) (Satoh et al., 2006) and *Apteronemobius asahinai* (Orthoptera) (Satoh et al., 2008)). The collembolan *Anurida maritima* (Guérin-Méneville, 1836) (Fig. 1), which is among the most numerous intertidal animals worldwide, is part of the latter group (Dexter, 1943; Joosse, 1966; Manica et al., 2000). It is a terrestrial species found in the upper intertidal zone where it feeds on dead and decaying matter. It forms large aggregations in cracks and cavities in the substrate whilst not foraging (Dexter, 1943; Imms, 1906). In these refugia the animals survive tidal submergence, moult, and reproduce (Joosse, 1966).

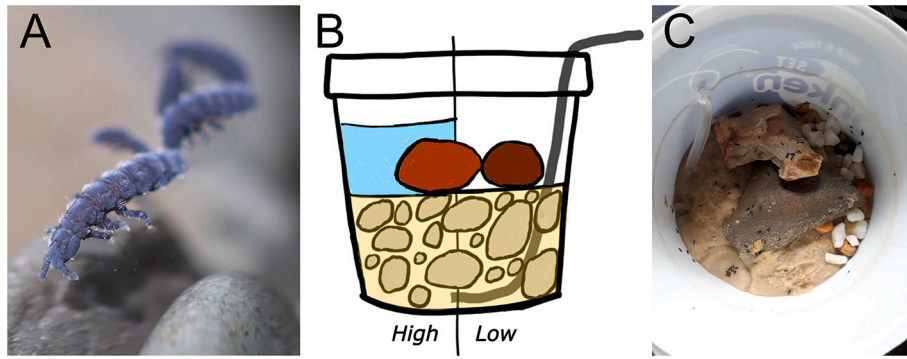In contrast to some other species of the intertidal zone (e.g. Evans,

Fig. 1. Species subject to investigation and the artificial environments (test chambers) used. A: *Anurida maritima* (Guérin-Méneville, 1836) floating on a small rock pool. Adult *A. maritima* measure 2–3 mm in length (Imms, 1906). B: Schematic drawing of the 1 l plastic pots ('test chamber') used to manipulate water levels. C: Image of a test chamber.
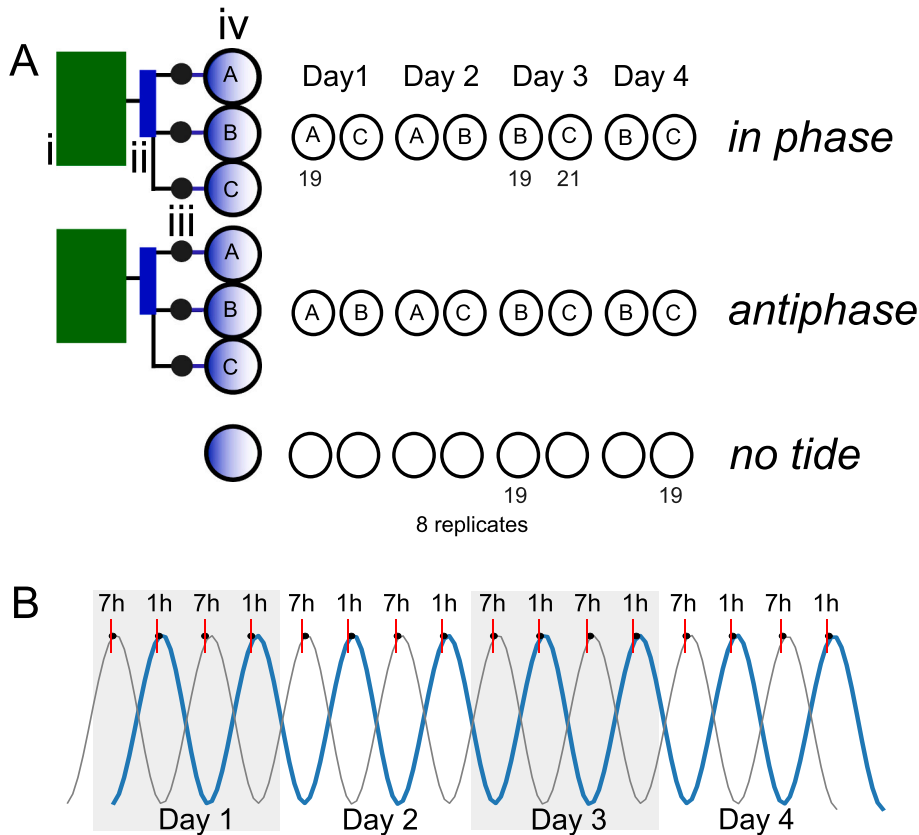

Fig. 2. Experimental setup used and number of replicates included. A) Schematic drawing of the system used and replicates taken. i) Raspberry Pi Zero that controls ii) relays to activate iii) peristaltic dosing pumps to control water levels in three iv) test chambers. Images not to scale. The circles on the right indicate time-lapse replicates with letters (A, B, C) indicating from which test chamber a replicate was taken. Numbers indicate how many individuals were included when deviating from 20. **B)** Schematic overview of the water levels in the *in phase* (blue) and *antiphase* (grey) replicates. The simulated high and low tides of the *in phase* replicates are aligned to tide times at Goldhanger (Maldon, UK). The vertical red lines indicate either 7 h or 1 h before high tide at Goldhanger. The black dots indicate time points of time-lapse images that were included in the statistical analyses. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

1976), *A. maritima* displays both nocturnal and diurnal foraging behaviour (McMeechan et al., 2000). Foraging activity seems aligned only to the tides and shows strong rhythmicity; animals leave their aggregations after high tide and return one hour before high tide at the latest (Foster and Moreton, 1981). This recurring cycle is endogenously controlled and runs freely for at least 7 days (McMeechan et al., 2000).

Endogenous biological rhythms are kept in pace by external cues (Zeitgebers) in a process that is called *entrainment* (Schmal et al., 2020). Important Zeitgebers are light and temperature (Beer and Helfrich-

Förster, 2020). The Zeitgeber that entrains the circatidal rhythm in *A. maritima* is not known. A significant and regular environmental change for *A. maritima* is inundation. It is the case that other organisms, such as the terrestrial Mangrove cricket (*Apteronemobus asahinai*) have circatidal rhythms entrained by submergence (Sakura and Numata, 2017; Satoh et al., 2008). This has not been tested empirically in marine collembola. In addition, it remains unknown if the rhythm displayed can synchronise with shifted tidal regimens. To investigate whether periodic inundation indeed functions as a Zeitgeber and entrains *A. maritima*'s

aggregation behaviour, artificial tidal environments were constructed and time-lapse photography was applied. These studies provide a better understanding of *A. maritima*'s circatidal behaviour and its response to changing environmental conditions.
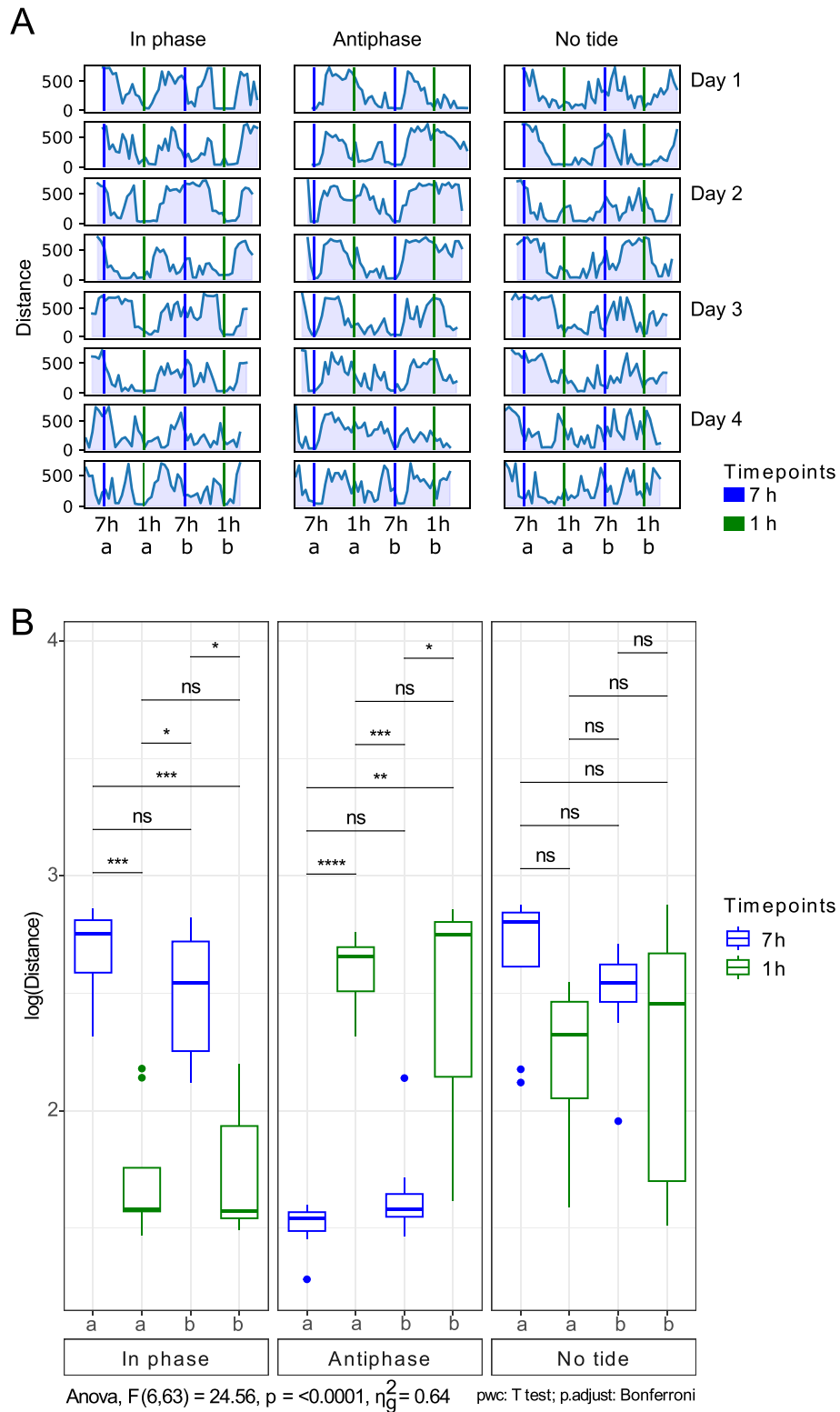

Fig. 3. Aggregation behaviour in *Anurida maritima*. A) Mean Euclidian distance between individuals in a Petri dish plotted against time for left: *in phase*, middle: *antiphase* and right: *no tide* treatments. Blue vertical lines indicate 7 h before Goldhanger high tide, green vertical lines indicate 1 h before Goldhanger high tide. **B)** Results of two-way mixed ANOVA and posthoc tests testing the different time points within each treatment. (a) before first simulated high tide (HT), (b) before second simulated high tide. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2. Methods

2.1. Animal collection

Animals were collected using an aspirator (entomological pooter) on the 19th of July 2023 at Goldhanger (Maldon, UK; 51°44′25.9″N 0°45′54.1″E) and transported to the laboratory in plastic containers. Animals from this location have previously been shown to belong to the *bisetosa* lineage (Timmermans et al., 2022; see also Arbea, 2001; Goto and Delamare-Deboutteville, 1953). The animals were transferred to 1 l plastic pots filled with children's play sand (Vital Earth Sales Ltd., Doncaster, UK) that was wetted with sea water and fed ad libitum amounts of Goldfish and Coldwater Flake Food (Mars Petcare, UK) on a daily basis.

2.2. Test chambers and experimental treatments

Artificial environments that allowed manipulation of water levels ("test chambers") were constructed. Each test chamber consisted of a 1 l plastic pot partly filled with play sand and small pieces of rock (Fig. 1). Water levels were manipulated using Raspberry Pi Zero computers (RPi) controlling 5 Volt peristaltic dosing pumps (ADA3910; Adafruit industries). One RPi controlled three pumps (i.e. three test chambers) using an 8-channel 5 Volt relay board module (Fig. 2A). Natural sea water, taken from the Goldhanger sample location, was pumped to and from each test chamber and a common storage container through silicone tubes (4 mm diameter). Direction of water movement was regulated using a Python script that switched relays on and off at set times. One hour before high tide, sea water was pumped into the test chamber (for 240 s) and one hour later the water was pumped out of the test chamber at similar speed.

Two days after field collection, 100 individuals were placed into each test chamber. Two distinct tidal timing regimens were applied: In the first regimen, one RPi controlled the inundation schedule based on the predicted high tides for Goldhanger, the sample location, using data from https://tides.willyweather.co.uk. In the second regimen, another RPi gradually shifted the inundation timing, advancing the pumping cycle by 15 min with each high tide. This incremental shift was carried out over 12 days, resulting in a 6-h phase shift, or approximately half a tidal cycle. By the end of this period, the first group remained synchronised with the natural Goldhanger tides, while the second group was in antiphase. Thus, the 'in-phase' group experienced high tide when the 'antiphase' group experienced low tide, and vice versa (Fig. 2B). No further shifts were applied. Animals were kept in the test chambers for at least an additional four days, after which aggregation behaviour was analysed using time-lapse digital photography.

2.3. Time-lapse digital photography and aggregation behaviour

Ideally, rhythmic behaviour should be studied on an individual basis. However, as aggregation can only occur when animals are part of a group, the rhythmic behaviour was analysed on a group basis. To investigate aggregation behaviour over the tidal day, a sample of animals was transferred to Petri dishes and monitored using digital photography. Animals of both treatments (*in phase* and *antiphase*) and the animals that had been kept in the original storage container throughout the experiment (third treatment: *"no tide"*; Fig. 2A) were included. Two replicate samples were obtained for each of the three treatments for four days, taking 20 new animals (but see Fig. 2A) from one of the test chambers for a total of 8 replicates per treatment. For each replicate, animals were placed on filter paper wetted with sea water in 90 mm diameter Petri dishes. The Petri dishes were sealed with cling film. Pictures (2304 × 1296 resolution) were taken every 30 min for 24 h using a RPi Zero, the Camera Module 3, and a Lisiparoi LED Flash (Cyntech Components). The cameras were controlled using Python 3 and the Picamera2, time and schedule libraries, with the first picture

taken at 10.00 pm. All experiments were run at room temperature (i.e. temperature was not controlled) and in total darkness. Lights were turned on occasionally e.g. when the experiment was checked or when animals had to be fed or transferred to Petri dishes.

Aggregation behaviour was assessed for each time point by calculating the mean Euclidian distance (in pixels) between all animal pair combinations within a dish. The digital images were opened in ImageJ 1.54f (Fiji win64 distribution) and the position (coordinates) of each of the animals was recorded using the multi-point tool. In case individual animals could not be discriminated because they were part of an aggregation, a random position within the aggregation was recorded. For some replicates a small part of the Petri dish was accidentally not included in the image for a subset of the time. If in these cases not all animals could be recorded, they were assumed to be within the area that was not visible. In addition, for one replicate the camera failed for a single time point (day 2, *in phase*, 6.00 am). For each image, the coordinates were exported and the mean Euclidian distance between each of them calculated using the pdist function of Python's SciPy library. Distances were plotted using Python's Matplotlib library

2.4. Statistical analyses

If aggregation behaviour synchronises to shifted tidal regimens, aggregation levels are expected to differ between treatments at their respective artificial low and high tides. To test whether aggregation at the artificial high and low tides differed between treatments (*in phase, antiphase, no tide)*, a two-way ANOVA (Treatment X Time point) was used comparing the mean Euclidian distances. For the analysis, mean Euclidian distances obtained from replicates that came directly after 1 and 7 h before every Goldhanger predicted high tide were selected (Fig. 2B): The '1 hour before HT images' coincide with the time the *in phase* (Goldhanger aligned) samples would have experienced inundation in the test chamber when the animals are expected to be maximally aggregated (small mean Euclidian distance). The *antiphase* samples would have experienced a dry environment (low tide) with the animals expected to show limited aggregation (large mean Euclidian distance). The '7 hours before HT images' coincide with the time the *in phase* (Goldhanger aligned) samples would have experienced a dry environment in the test chamber (low tide; limited aggregation of animals; large mean Euclidian distance) and the *antiphase* samples would have experienced inundation (high tide; maximum aggregation of animals; small mean Euclidian distance). As the tidal period is 12.4 h, there were two '1 hour before HT' and two '7 hours before HT' time points per 24-h time-lapse recording. To determine whether all assumptions of the ANOVA were met, outlier, normality (Shapiro-Wilk normality test) and Homogeneity of variances and co-variances tests (Levene's test for equality of variances; Box's M) were first applied. Statistical analyses and data visualisation were performed in R 4.2.0 using the ggpubr, tidyverse, rstatix and tidyverse packages, as described on https://www.datanovia.com/en/lessons/mixed-anova-in-r/ (last accessed 14/12/2023).

3. Results

3.1. Aggregation behaviour

Aggregations with exuviae were formed in all test chambers, mimicking natural *A. maritima* behaviour. Aggregation level (defined by the mean Euclidian distance between animals in a Petri Dish) fluctuated over the 24-h time-lapse intervals (Fig. 3). Animals subject to the *in phase* (aligned to Goldhanger) treatment, were most strongly aggregated around Goldhanger's predicted natural high tides (Fig. 3A, left column). In contrast, animals subject to the *antiphase* treatment, were not strongly aggregated around Goldhanger's high tides. Instead, these animals showed high levels of aggregation at their new, artificially shifted simulated high tides (Fig. 3A, middle column). A 6-h shifted high tide roughly coincided with Goldhanger's low tide, implying the aggregation

Table 1
Results of two-way mixed ANOVA and posthoc tests. 1 A: Two-way interactions between treatment and time point. 1B: Results of post-hoc test (one-way ANOVA, Bonferroni corrected *p*-values) for between group (i.e. between treatment) differences at each of the four time points. 1C: Results of post-hoc tests (pairwise *t*-test, Bonferroni corrected p-values) for treatments within each of four time points. 1D: Results of post-hoc tests (one-way ANOVA, Bonferroni corrected p-values) for effect of time for each of the treatments. (a) before first simulated high tide (HT), (b) before second simulated high tide. Dfn: degrees of freedom for the numerator of the F ratio, Dfd: degrees of freedom for the denominator of the F ratio, F: F value, ges: generalized eta-squared, adj.p: adjusted *p* value.

A	Effect	Dfn	Dfd	F	ges	P
	Group	2	21	11.026	0.200	**5.32×10^{-4}**
	Time	3	63	0.744	0.026	5.30×10^{-1}
	Group:Time	6	63	24.559	0.641	**8.79×10^{-15}**

B	Time	Effect	Dfn	Dfd	F	ges	p.adj
	7 h before HT (a)	Group	2	21	71.154	0.871	**1.77×10^{-9}**
	1 h before HT (a)	Group	2	21	21.065	0.667	**3.83×10^{-5}**
	7 h before HT (b)	Group	2	21	33.241	0.76	**1.24×10^{-6}**
	1 h before HT (b)	Group	2	21	5.808	0.356	**4.00×10^{-2}**

C	Time	Group 1	Group 2	p.adj
	7 h before HT (a)	In phase	Antiphase	**2.82×10^{-9}**
		In phase	No tide	1.00
		Antiphase	No tide	**3.82×10^{-9}**
	1 h before HT (a)	In phase	Antiphase	**6.14×10^{-6}**
		In phase	No tide	**4.67×10^{-3}**
		Antiphase	No tide	**2.93×10^{-2}**
	7 h before HT (b)	In phase	Antiphase	**1.55×10^{-6}**
		In phase	No tide	1.00
		Antiphase	No tide	**1.91×10^{-6}**
	1 h before HT (b)	In phase	Antiphase	**9.91×10^{-3}**
		In phase	No tide	8.65×10^{-2}
		Antiphase	No tide	1.00

D	Group	Effect	DFn	Dfd	F	ges	p.adj
	In phase	time	1.69	11.8	30	0.771	**1.10×10^{-4}**
	Antiphase	time	3	21	32.8	0.781	**1.24×10^{-7}**
	No tide	time	3	21	2.29	0.198	$3.24 \times 10{-1}$

behaviour of these two treatments was indeed in antiphase. Aggregation of animals not exposed to rhythmic inundation (*no tide* treatment), no longer accurately followed the Goldhanger predicted natural tides (Fig. 3A, right column).

3.2. Statistical analyses

A two-way mixed ANOVA was performed to support above observations. Analyses of untransformed data revealed several outliers, deviations of normality (Shapiro-Wilk test) and non-homogeneity of variances (Levene's test). In an attempt to meet the assumptions, the data was $\log_{10}$-transformed. $\log_{10}$-transformed data variances (Levene's test) and co-variances (Box's M test) of different treatments were not significantly different from each other, but outliers and deviations from normality were still detected (Supplementary data). All outliers were reviewed and deemed to be valid data points. Hence, it was decided to not remove them from further analyses.

The ANOVA revealed significant two-way interactions between treatment and time points (Table 1A). Subsequent, post-hoc tests revealed significant between-group (i.e. between treatment) differences

at each of the four time points (Table 1B), supporting the observation that the mean distance between animals (i.e. amount of aggregation) at each time point is affected by inundation regimen.

This is further supported by the observation that treatments within each of the four time points were deemed significantly different in most cases, including all comparisons between the *in phase* and *antiphase* treatments (Table 1C; Supplementary data). This also supports the above suggestion that these animals' rhythms are in antiphase.

When comparing time points for each treatment, significant differences were observed for the *in phase* and for the *antiphase* treatments, but not for the *no tide* treatment (Table 1D). When testing the different time points within each treatment (Fig. 3B), no differences were observed between the two '1 hour before HT' and the two '7 hours before HT' time points for both the *in phase* and the *antiphase* treatments. However, significant differences were observed between all '1 h before HT' - '7 hours before HT' pairwise comparisons for these two treatments. No comparisons involving *no tide* treatment were significant, suggesting aggregation levels no longer differed between high and low tide.

4. Discussion

Various intertidal animals have evolved an ability to anticipate tidal change. *Anurida maritima* displays endogenously controlled aggregation behaviour that is closely aligned to the tidal cycle (Foster and Moreton, 1981; McMeechan et al., 2000). The results presented here indicate that this rhythmic aggregation behaviour is not imprinted during (early) development, but that it depends on continuous regular inundations and entrains to shifted rhythms. This implies that rhythmic aggregation behaviour in *A. maritima* is responsive to environmental cues and that inundation acts as a key Zeitgeber.

These observations open up opportunities for more detailed research on the chronobiology of the species. The regulation of circatidal rhythms remains elusive and over the years various hypotheses have been put forward to explain them (Häfker et al., 2023; Rock et al., 2022). These include the circalunidian hypothesis, that assumes there to be two ~24.8 h endogenous mechanisms that run in antiphase (Palmer, 1995); the bimodal clock hypothesis, that assumes there is only one 'timing mechanism' that can change frequency by switching Zeitgeber (Enright, 1976); the circatidal/circadian clock hypothesis, that assumes there is a ~ 12.4 h circatidal clock that runs independently of a 24 h circadian clock (Naylor, 1996). Support for the bimodal clock hypothesis comes for example from a study on the oyster, *Crassostrea gigas* that showed that genes that in other organisms function as circadian clock genes can be expressed at circatidal frequency in a tidal environment (Tran et al., 2020). Support for the circatidal/circadian clock hypothesis comes, for example, from gene expression studies on tidal and non-tidal freshwater snail populations, *Semisulcospira reiniana* (Yokomizo and Takahashi, 2024), or from studies that interfered with the expression of known circadian clock genes using dsRNAi in *A. asahinai* and *Eurydice pulchra* (Takekata et al., 2012; Zhang et al., 2013). These latter studies revealed that the gene expression interference disrupted circadian rhythms, yet left circatidal rhythms unaffected. Interestingly, a close molecular link between circadian and circatidal behaviour has recently been described via the transcription factor Bmal1 (CYCLE). *Bmal1* is a core circadian clock gene, but disruption of its expression via dsRNAi or CRISPR-Cas9 genome editing was shown to strongly affect circatidal rhythms in the crustaceans *Eurydice pulchra* and *Parhyale hawaiensis* respectively (Kwiatkowski et al., 2023; Lin et al., 2023). These studies consequentially revealed the first gene involved in circatidal rhythms and provided empirical evidence that the circadian and circatidal timing mechanisms are separate, but share components.

Like most shorelines around the world, coastal regions in the United Kingdom, including the location sampled here (Goldhanger, Maldon, UK), experience two high and two low tides per day (semidiurnal tides). However, other tidal patterns exist, including diurnal (one high and one low tide per day) and mixed ones (alternating between diurnal and
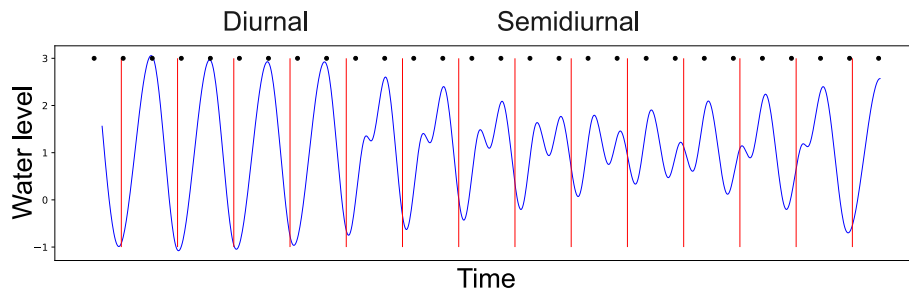
Fig. 4. Conceptual drawing showing tidal regimen for a coastal area with mixed tides. The blue line shows an example of mixed tide, switching between semidiurnal and diurnal patterns, for Sanibel Island (Florida, USA). The image represents 14 days, with days separated by vertical red lines. Black dots are 12.4 h apart and represent semidiurnal high tides as experienced by most coastal regions, including Goldhanger (Maldon, UK). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

semidiurnal on a weekly basis) (Stillman and Barnwell, 2004). Diurnal and mixed tides are found, for example, in the Gulf of Mexico and the West Coast of Florida (USA), respectively. To our knowledge, it remains currently unclear how animals experiencing such mixed tides anticipate upcoming change. Although mixed tides vary in their period over time, they include a predictable diurnal component with high tides ~24.8 h apart (Fig. 4) and it could be hypothesised that such species rely on a single daily cue to entrain their circatidal rhythms. The question then arises, however, if organisms distinguish semidiurnal and diurnal tides, or remain synchronised to the semidiurnal pattern even in the absence of inundation in diurnal weeks. The flexibility of our set-up, which is controlled by a small programmable microcomputer, will allow in-depth investigation of *A. maritima*'s response to alternative tidal regimes. Such studies should include species that are naturally exposed to mixed tides, such as the congeneric *A. ashbyae* (a species that is morphologically almost indistinguishable and often confused for *A. maritima*) that has been reported from various foreshore locations in Florida (Christiansen and Bellinger, 1988).

The results presented here show that recurrent inundation entrains circatidal aggregation behaviour in *A. maritima*. This implies that *A. maritima* will be able to adjust its rhythmic behaviour, for example, to tide shifts imposed by coastal or climate change, or after drifting to other coastal areas. The exact cue used for entrainment remains unknown. In the mangrove cricket *A. asahinai* direct contact with water functions as Zeitgeber (Sakura and Numata, 2017), but this is unlikely true for *A. maritima* as the species is well known to float on the surface of small pools of water during low tide (Imms, 1906). During submergence, *A. maritima* is exposed to reduced oxygen availability (Zinkler et al., 1999), and other environmental factors, such as gas concentrations and pressure, could be reliably used to synchronise to the tides (Wilcockson and Zhang, 2008). Further study is needed to determine which exact cues *A. maritima* uses to coordinate its aggregation behaviour and shed further light into this fascinating adaptation to the ever-changing intertidal environment.

5. Conclusions

Anurida maritima has been long known to display circatidal activity rhythms (Foster and Moreton, 1981). Here we present a simple set-up that enables simultaneous, multiple replicate manipulation and testing of behaviour in littoral maritime taxa and show that in *A. maritima* the external cue that entrains the rhythm is linked to inundation. In the absence of regular inundation of the environment, the circatidal rhythm will no longer be accurately synchronised with the tides. In addition, the rhythm can be shifted by artificially shifting the timing of the inundation. This implies the species can respond to adjusted tide times, for example when colonising new coastal areas, or to those imposed by coastal or climate change. The results presented form a strong basis for more detailed chronobiological research on *A. maritima* with the ultimate aim to gain a deeper understanding of biological time-keeping.

CRediT authorship contribution statement

Martijn J.T.N. Timmermans: Writing – original draft, Software, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Madeleine King:** Methodology, Conceptualization. **Diane Purchase:** Writing – review & editing, Resources, Conceptualization. **Benjamin J.A. Dickins:** Writing – review & editing, Formal analysis. **Thomas E. Dickins:** Writing – review & editing, Formal analysis, Conceptualization. **Stephen Kett:** Writing – review & editing, Resources, Methodology, Conceptualization.

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.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jembe.2024.152062.

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