# ENDOGENOUS CIRCATIDAL ACTIVITY RHYTHM IN A LITTORAL MITE, *BDELLA SEPTENTRIONALIS* (ACARINA, BDELLIDAE)

BY H. ERNST *

ACARI
LITTORAL
TIDAL
ACTIVITY
RHYTHM
BDELLIDAE

SUMMARY : The intertidal mite, *Bdella septentrionalis* Atyeo & Tuxen, inhabits the upper eulittoral and supralittoral of brackish to euhaline rocky seashores and estuaries. Mites are only active during days and on surfaces wettened by seawater (tidal submerging/spray-water). The activity of *B. septentrionalis* along the Weser estuary correlates with the tide. In the laboratory the same species, from the same locality, shows a 12-hour periodicity in its activity when exposed to constant artificial light. An endogenous circatidal rhythm seems likely. In contrast, *B. septentrionalis* originating from the Baltic Sea do not exhibit any such activity pattern under the same laboratory conditions. A model for the interaction between tidal activity rhythm and the light-dark cycle is given.

ACARI
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BDELLIDAE

ZUSAMMENFASSUNG : Die Schnabelmilbe *Bdella septentrionalis* Atyeo & Tuxen besiedelt das obere Eulitoral und das Supralitoral brackischer bis mariner Felsküsten und Ästuare. Die Milben sind während des Tages auf vom Seewasser befeuchteten Oberflächen nach tidaler Überflutung/Spritzwasser aktiv. Die Aktivität von *B. septentrionalis* im Weserästuar ist tidenabhängig. Tiere vom Weserästuar zeigen im Labor unter konstanten Bedingungen und Dauerhell eine zwölfstündige Periodizität in ihrer Aktivität. Ein endogener circatidaler Rhythmus ist anzunehmen. Im Gegensatz hierzu zeigen Tiere von *B. septentrionalis* von der Ostsee keinen erkennbaren Aktivitätsrhythmus unter den selben Laborbedingungen. Es wird ein Model für die Interaktion zwischen tidalem Aktivitätsrhythmus und dem Hell-Dunkel-Zyklus vorgeschlagen.

ACARIEN
LITTORAL
ACTIVITÉ LIÉE
À LA MARÉE
BDELLIDAE

RÉSUMÉ : L'acarien de la zone de balancement des marées, *Bdella septentrionalis* Atyeo & Tuxen, habite les rives maritimes et les estuaires rocheux saumâtres à euryhalines de l'eulittoral supérieur et du supralittoral. Les acariens ne sont actifs que pendant la journée, et sur les surfaces arrosées par l'eau de mer (eaux submergeantes/arrosantes de la marée). L'activité de *B. septentrionalis* dans l'estuaire de la Weser est liée à la marée. En laboratoire, cette espèce récoltée dans la même localité, montre en lumière artificielle constante une périodicité d'activité de 12 heures. Un rhythme endogène circatidal semble probable. Par contre, *B. septentrionalis* de la Mer Baltique dans des conditions de laboratoire identiques, ne présente pas un tel exemple d'activité. Un modèle de l'interaction entre le rhythme d'activité lié à la marée et le cycle lumière/obscurité est proposé.

* Department of Biology, University of Bremen, Leobenerstr, 28359 Bremen, Germany.

## Introduction

Mites are an important part of the intertidal fauna of rocky seashores. Sometimes they comprise more than 90 % of the entire arthropod fauna (Schuster, 1965). A very common species in the littoral zone of northern Germany is *Bdella septentrionalis* (identical to *Bdella longicornis* in Alberti, 1973 : personal communication) which inhabits brackish to euhaline rocky shores. It occurs from the upper eulittoral to the lower supralittoral. In periods of submergence (high tide), *Bdella septentrionalis* moves into cracks.

Fertility, tolerance to submergence and tolerance to different salinities are important for survival of mites in the intertidal zone (Weigmann, 1973). These mites also need to adjust their activities to the variable pattern of tidal submergence (Treherne and Foster, 1978).

Detailed studies on the activity rhythm of mites in the intertidal zone are rare. The present study investigates the activity rhythms of *Bdella septentrionalis* and compares populations of the Weser estuary where there is a high tidal range with populations of the Baltic Sea with a low tidal range. Laboratory studies were carried out to reveal whether immigration of species of Bdellidae into rocky seashores resulted in establishing an endogenous circatidal activity rhythm. A further question is whether this tidal activity pattern has been modified in populations of the Baltic Sea, since they are isolated and not exposed to a significant tidal range ; the water level there is more dependent on wind direction and strength.

## Locations, Materials and Methods

Mites were identified after Atyeo (1960) and Atyeo and Tuxen (1962).

Studies were carried out at two different locations.

Site I is characterised by a high tidal range of approximately 4 m. It is located in the Weser estuary near Bremerhaven/Weddewarden. The " rocks " of this rocky shore are remains of the Fortress Brinkamahof II. They consist of parts of the former defence wall (sand stone), inner wall fragments (bricks), large pieces of concrete, and elements made from a mixture of cement and brick. The fortress is located in the brackish zone (salinity of about 5-16 ‰ S). This site is characterized by the presence of pronounced zonation in the littoral zone. Detailed investigations were carried out mainly on one particular boulder that was highly exposed to wind and wave action. This boulder consists of coarse concrete and is covered with the green algae *Blidingia minima.*

Site II is located on the western shore of the Kieler Aussenförde in the Baltic Sea. Several rocky breakwaters protect this site against wave action. The largest breakwater is approximately 80 cm high, 4 m wide and 50 meters long, facing towards the southeast. The breakwater is built from large natural rocks, joined together by concrete at some places. The tidal range at this location of the Baltic Sea averages 10 cm, with large variations caused by wind (maximum water level during observation was 1 meter above m.s.l.). The salinity of sea water is about 16 ‰ S. The zones of the littoral are marked. The orange-lichen zone (supralittoral) is only present in a few areas, e.g., at the entrance of the northeastern side. The examined boulder consists of slate with numerous cracks. It is located on the upper half of the northeastern side. The surface is covered with the green algae *Blidingia minima* and *Prasiola* sp.

On site I, daily observations were made in the period from 22 May to 9 June 1989, between 4 a.m. and midnight, and from 29 August to 6 September 1989 between 7 a.m. and 8 p.m. On site II, daily observations were made in the period from 14 June to 6 July 1989 between 4 a.m. and 11 p.m., and from 12 to 16 September 1989 between 7 a.m. and 8 p.m. Furthermore, on both sites observations were made in monthly intervals from January to December 1989.

The following measurements and parameters were obtained at hourly intervals : number of active individuals of *Bdella septentrionalis* separated into different instars, light intensity 25 mm above the surface in KLux, air temperature 10 mm above the surface in °C, surface temperature in °C , humidity 10 mm above the surface in % RH, estimate of surface wetness (submerged, wet, wet to moist, moist, damp, dry), water level in cm in relation to mean seawater level (m.s.l.), height of surf in cm, and wind force 1 metre above the boulder.

Laboratory experiment : an artificial habitat was constructed inside an aquarium. Materials (rocks, seawater) were obtained from the original location on the day of animal collection. The aquarium was filled with seawater to a level of 5 cm. After 40 adults had been placed into this aquarium, it was covered with a glass screen. The temperature within the aquarium was 15°C and humidity approximately 100 % RH. The animals were exposed to constant artificial day light. The light intensity 10 mm above the examined surface was 1 KLux. A camera with a macro lens and flash was mounted above the aquarium and pictures were taken automatically at 20 minute intervals over a period of 8 days. Subsequently the number of mites in each picture was counted.

## Results

Field studies :

The observed activity of *Bdella septentrionalis* in the habitat was usually related to feeding. On most occasions they were seen hunting solitarily on vertical surfaces covered with *Blidingia*. Animals were only active on surfaces that were moistened by seawater. A surface wettened by rain water or a totally dry surface inhibited any activity of the mites. During periods of submergence, darkness or low humidity (below 70 % RH) the mites moved into cracks. These cracks were also used for ovation and desquamation of larvae and nymphs. Mites avoided high intensities of light and surface temperatures above 20°C.

Site I (littoral zone with high tidal range) : animals were only active after submergence or at neap-tides after the surface had become wettened by high surf. In May/June a maximum of 18 individuals (adults and larvae ; nymphs were not found at this season) were active on the examined surface. Main activity was at dawn and dusk, while in total darkness individuals remained inactive. Only on 31 May and 2 June a few mites were active during midday when the weather was fairly cold and the surface did not dry out totally between the tides. Activity began 1 to 2 hours after high tide, peaked four hours after high tide and declined as the surface dried (see Fig. 1). Variations can be correlated with the height of the preceeding tide. The interval between high tide and the start of activity was much shorter than the period between the time when the animals moved into cracks and the following high tide. In August/September a maximum of 62 individuals (adults, trito- and deutonymphs) were observed on the same surface. During this season most of the animals were found active on rocks at midday during periods of low tides. When high tides occurred during night, the start of activity was delayed until the morning hours (see e.g. 4th September 1989, Fig. 2), or the animals remained inactive under unfavourable conditions, e.g. because of a dry surface (see e.g. 4th June 1989, Fig. 2). Activity commenced after the boulder emerged from the retreating tide. The end of the individuals activity (indicated by their dissappearence) occurred much earlier in comparison to the start of activity when relating start and end of activity to the water level.

Site II (littoral zone with a low tidal range) : *Bdella septentrionalis* on the Baltic Sea is day-active. Animals were only active on surface that was wettened by seawater (spray-water), as was also found for the population at the Weser estuary. During the observation period from 14th June to 6th July 1989, the weather was hot and dry. Surface temperatures peaked at midday with values around 38°C, and air humidity was under 40 % RH for most of the time. *Bdella septentrionalis* was only observed on 3rd July, 1989, at dusk. This day was characterized by a high seawater level and related to that a high surface wetness. A suprisingly high number of 25 individuals, all being adults, were counted. From 12th to 16th September adults, trito- and deutonymphs were seen, with an average daily maximum of 22 animals. Adults and tritonymphs were observed at any time of the day with a maximum abundance at 4 p.m (see Fig. 3). Adults and tritonymphs were found on wet surfaces as well as damp surfaces where deutonymphs were

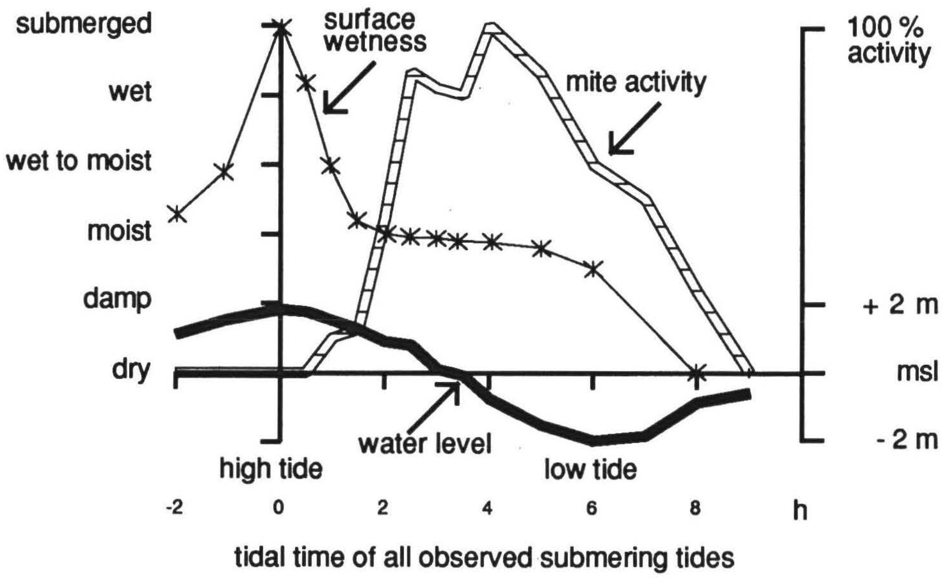


FIG. 1 : Activity of *Bdella septentrionalis* between 22nd May and 9th June, 1989, in Weddewarden for all submerging tides, averaged on one hypothetical tide (high tide = 0) in relation to surface wetness and water level. Water level given in metres above/under mean seawater level (m.s.l.).

active on moist surfaces only. The small changes of seawater level (~ 10 cm) and of temperatures had no significant effect on activity of the animals. The main periods of acitivity were associated with a humidity of 80-90 % RH. Light intensity during acitvity ranged from 0.2-10 KLux.

Observations in the laboratory : From the first day of observation *Bdella septentrionalis* from the Weser estuary showed two well-defined peaks of spontaneous activity. In the first three days the spontaneous frequency of activity was slightly irregular (transient) but occurred in intervals of about 12.5 hours. On the fourth day of observation a stable activity rhythm with 12 hour intervals was established (see Fig. 4). Towards the end of the experiment, the activity decreased slightly. In contrast, animals from the littoral with a low tidal range from the Kieler Förde did not establish a recognizable rhythm under the same conditions. The activity level was relatively high during the first few days of observation, and decreased slightly towards the end of the study.

## DISCUSSION

Locomotor activity of *Bdella septentrionalis* at the Weser estuary follows a tidal rhythm. The amplitude of activity peaks is primarily determined by the amount of surface wetness. Acitvity is limited to periods after high tide. Animals are active only on damp to wet surfaces. In summer, low tide at midday and neap-tides result in quick drying of the surface. The dry surface inhibits activity. During summer main activity takes place at dusk and dawn. In autumn animals remain active also at midday. Furthermore, under favourable conditions, periods of activity can be adjusted between two adjacent high tides, resulting in synchronization to a circadian rhythm. RÜPPEL (1967) emphazises the importance of surface wetness as a dominant abiotic factor in the littoral. The results of the present study show a marked relationship between the salinity of the surface wetness and the activity of *B. septentrionalis*. Decrease of salinity (e.g. after rain) inhibits all activity. Salinity of the moist substrate is therefore considered the main determinant for the habitat restriction of the animals to the brakish to euhaline littoral.

In the laboratory *Bdella septentrionalis* from the Weser estuary showed a free-running circatidal activity rhythm. The activity periods in the laboratory were shorter than in the field where the activity was triggered by tide (period of about 12.42 hrs.). An endogenous circatidal activity rhythm seems

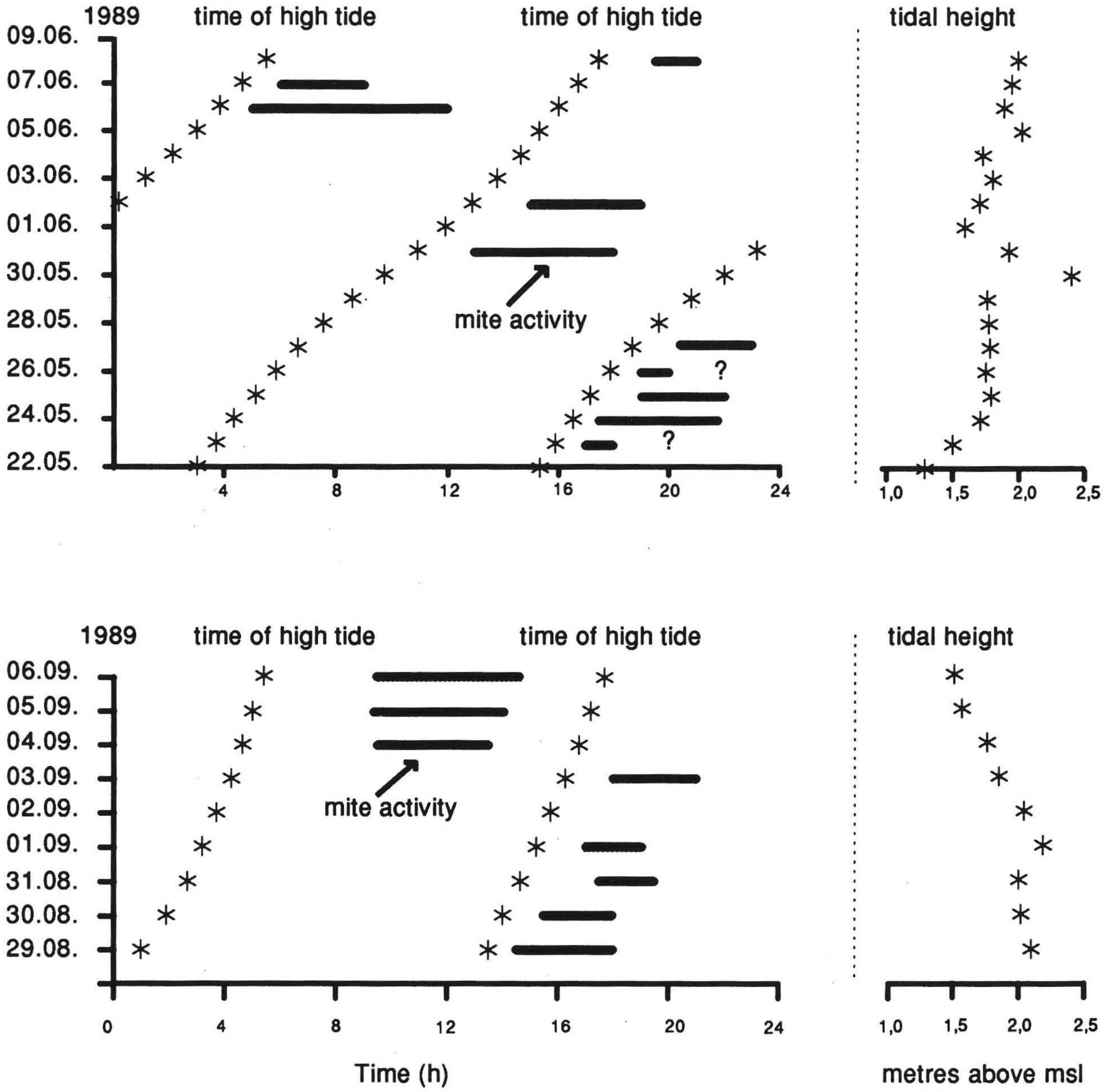


FIG. 2 : Activity of *Bdella septentrionalis* in relation to the timing of occurrence and height of high tides from 22nd May to 9th June, 1989, and from 29th August to 6th September, 1989 in Weddewarden. The horizontal bars represent the duration of mite activity. Height of tide are given in metres above mean seawater level (m.s.l.).

likely, as was also proposed for *Ameronothrus marinus* by SCHULTE (1976). In case of an exogenously controlled periodicity, the rhythm would be interupted under isolated conditions, according to the rules of ASCHOFF (1957). Individuals from the Baltic Sea show a diel rhythm in their natural habitat. However, in the laboratory under artificial light they did not show any rhythm. Therefore, the diel rhythm of these individuals appears to be triggered exogenously by day light. In contrast, *Ameronothrus marinus* from the Baltic Sea showed a 24-hourly rhythm in a similar experiment (SCHULTE, 1976).

FOSTER *et al.* (1979) investigated the activity rhythms of *Bdella interrupta* Evans which lives in marine saltmarshes. They described short-term

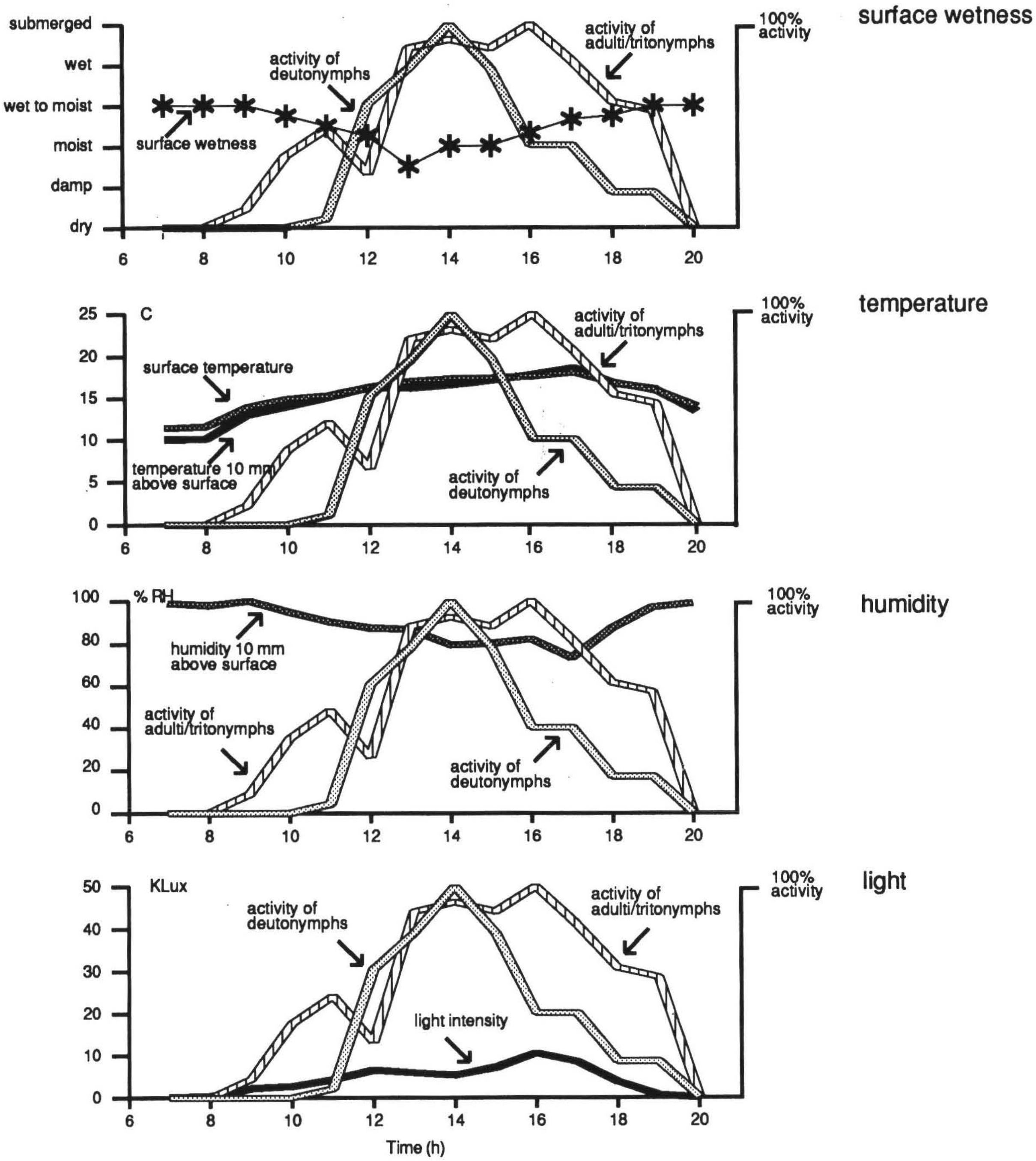


FIG. 3 : Activity of *Bdella septentrionalis* in relation to surface wetness, temperature, humidity and light intensity from 12th to 16th September, 1989, in Bülk at the Kieler Förde. Temperature given in °C, humidity in % RH and light intensity in KLux.

variations of activity rhythms following the change from spring tides to neap-tides. During periods of tidal submergence activity peaks had a period of 12.5 hours ; in the presence of non-submerging tides this period decreased to 11.5 hours. In isolated habitat portions in the field under natural light conditions, peaks were maintained with a period of almost exactly 12 hours. TREHERNE and FOSTER (1977) suggested a simple, circatidal rhythm to explain this observation. These authors found that

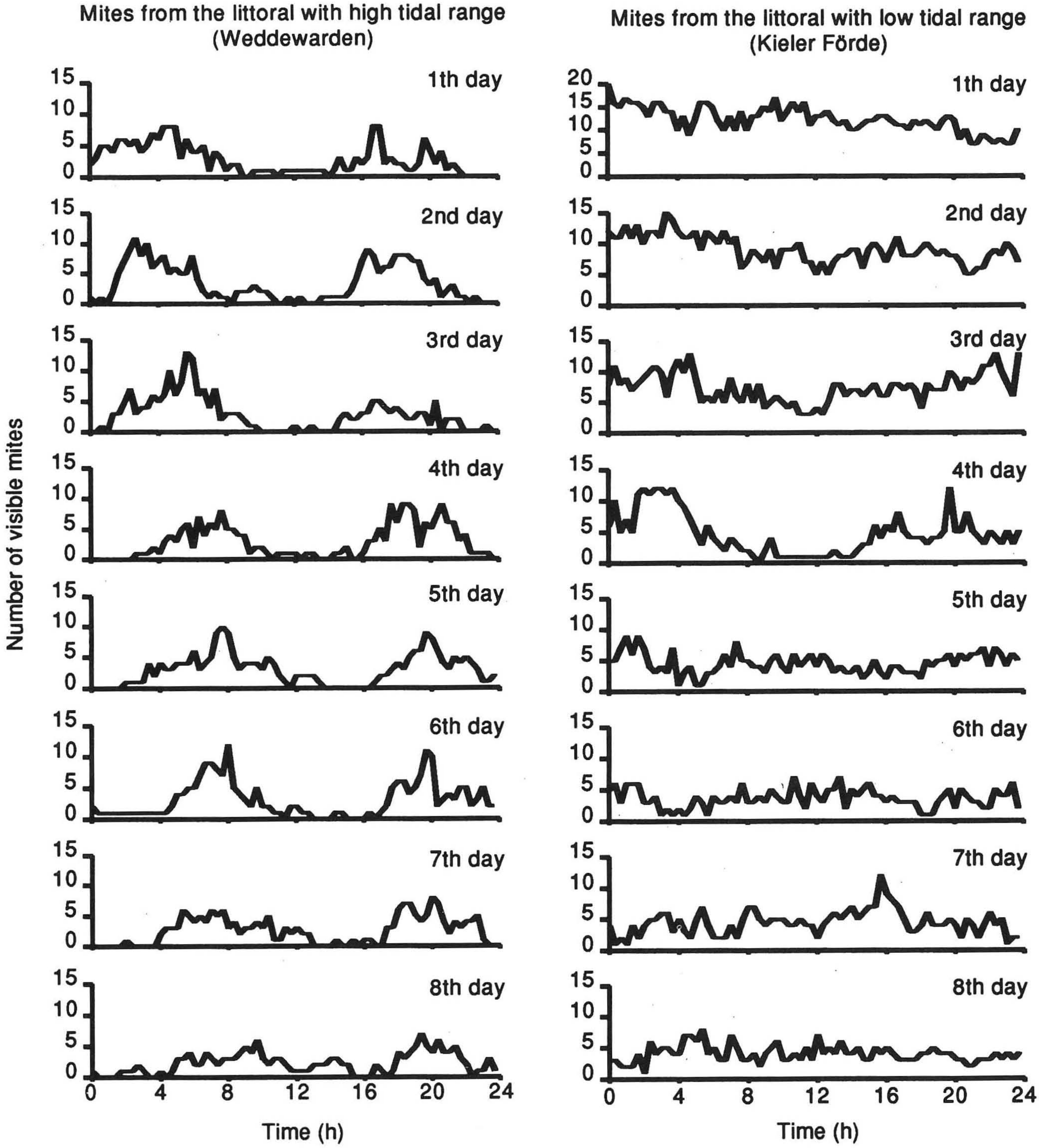


FIG. 4 : Locomotor activity of *Bdella septentrionalis* in the laboratory under constant light (1 KLux), constant temperature (15°C), saturated humidity and absence of tide from the littoral with high tidal range (Weddewarden) and from the littoral with low tidal range (Kieler Förde). Results are expressed as the total numbers of visible mites on the surface.

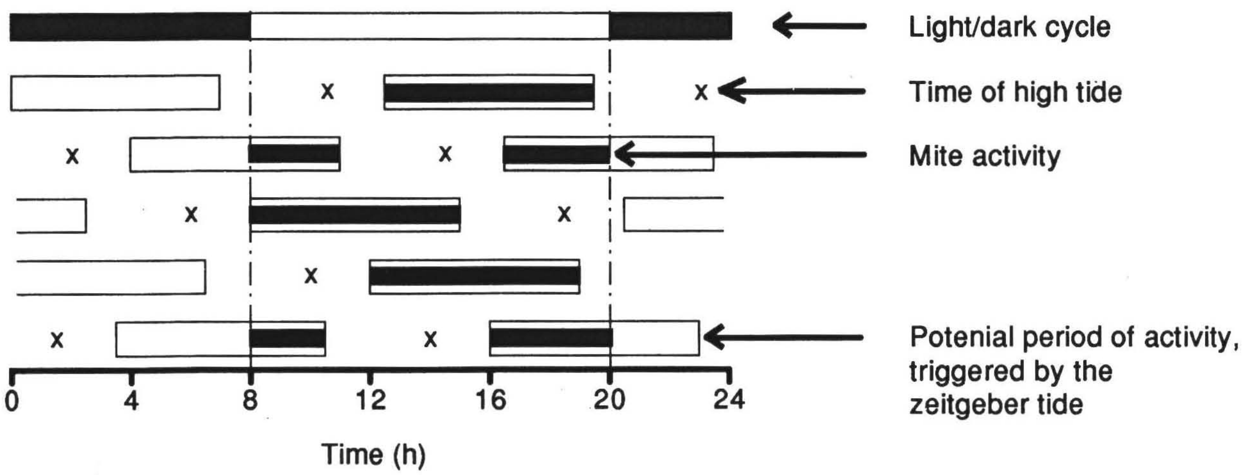


FIG. 5 : Model for the interaction between tidal activity rhythm and the light/dark cycle for *Bdella septentrionalis*, Weddewarden, under favourable surface wetness and other favourable microclimatic conditions.

in case of tidal submergence the period adopts a 12.5 hour period ; in absence of submergence (and of the external zeitgeber) free-running activity follows a 11.5 hour rhythm. In contrast, FOSTER *et al.* (1979) suggested the presence of a second zeitgeber. They assumed that after tidal submergence the activity rhythm follows a 12.5 hour period, and that during non-submergence (absence of the first zeitgeber) the rhythm is determined by a second zeitgeber (e.g. light/dark cycle). The creation of a stable relationship of periods with the light/dark cycle in absence of submergence supports this hypothesis.

For *Bdella septentrionalis*, the existence of two independent zeitgebers seems unlikely. In this species tides determine the periodicity of activity. In addition, the light/dark cycle will determine start and end of activity, but without changing the periodicity and not acting as a second zeitgeber. A model for the interaction between the tidal activity rhythm, triggered by the zeitgeber tide, and the light/dark cycle is presented in Fig. 5, presuming favourable surface wetness and microclimatic conditions similar to those in the observation period in autumn. A constant shift of tides by 4 hours (equaling a period of about 6 days in Weddewarden) and a regular 12 hourly day-and-night rhythm have been chosen to simplify the presentation. Adding abiotic factors which inhibit activity (dry surface, high temperature and low humidity at mid-day during summer) to the schematized graph (see Fig. 6), the shift of activity towards the hours around dawn and dusk becomes evident.

Light is generally accepted as a zeitgeber for rhythms with a daily periodicity. Nothing is known about the tide-dependent factors acting as a zeitgeber. Many factors are related to the changing water levels, such as temperature, hydrostatic pressure, intensity and spectral composition of light, vibrations of the substrate by surf, turbulences and under-water sound (BÜNNING, 1977). Furthermore, many species inhabiting the littoral are exposed to different tidal factors, depending on their habits and their preferred littoral zone. (LEHMANN *et al.*, 1974). LEHMANN *et al.* (1974) proved vibrations of the substrate to be a tidal zeitgeber in crabs (*Uca urvillei* and *Uca annulipes*). Substrate vibration is unlikely to act as a zeitgeber in *B. septentrionalis* since during field studies on the rear side of the fortress Weddewarden (absence of surf) *B. septentrionalis* was present in large numbers, and followed a tidal rhythm. It is also unlikely that the change between dry and wet surface represents a determining factor, because in autumn the surface did not dry between high tides. Regular submergence may act as a zeitgeber, as proposed for *Bdella interrupta* by FOSTER *et al.* (1979).

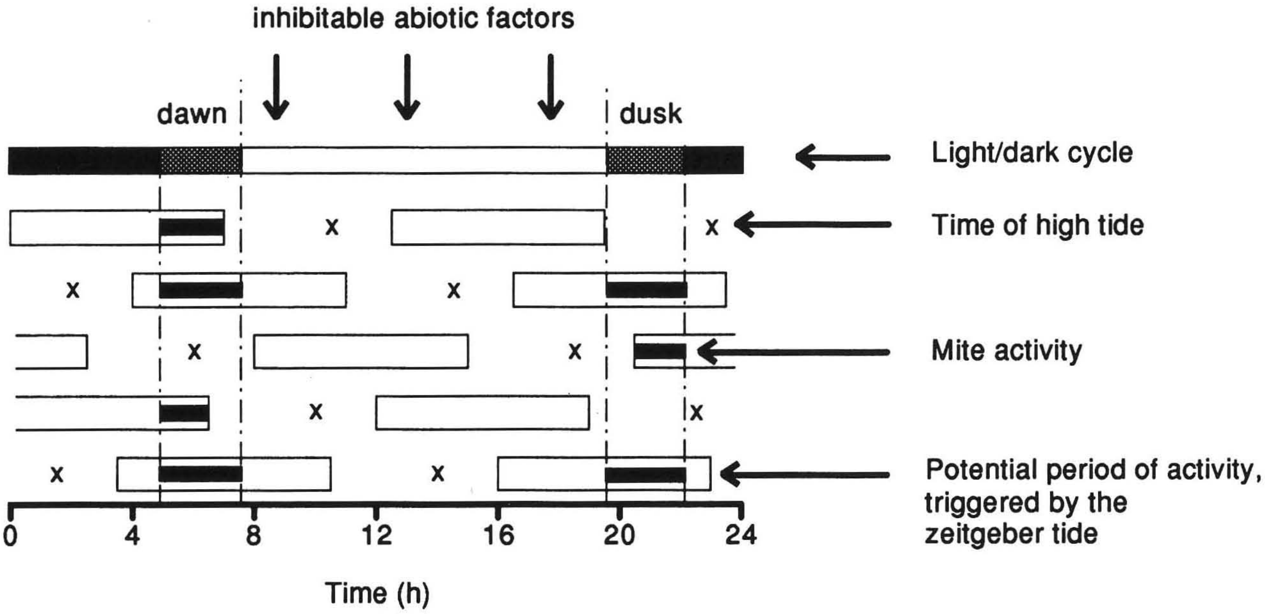


FIG. 6 : Model for the interaction between tidal activity rhythm and the light/dark cycle for *Bdella septentrionalis*, Weddewarden, under inhibitable abiotic factors during day time, such as high temperature, dry surface and low humidity.

## CONCLUSION

In adaption to the tidal regime zone, the ancestors of *Bdella septentrionalis* developed an endogenous, circatidal activity rhythm. This rhythm has been modified in the same mite species inhabiting the shores of the geologically younger Baltic Sea. With this region lacking a tide, here the activity of *B. septentrionalis* is triggered by exogenous factors, whereas the endogenous activity rhythm is lost.


## ACKNOWLEDGEMENTS

I would like to express my sincere thanks to : Prof. Dr. H. WITTE, University of Bremen, for critical discussions ; J. OTTO, CSIRO in Canberra, for critical discussions and translation support ; Prof. Dr. G. ALBERTI, University of Heidelberg, for the confirmation of the identification of *Bdella septentrionalis*.


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