Nocturnal surface activity of endobenthic nemertines on tidal flats

Martin Thiel¹, Walter Nordhausen² & Karsten Reise³
1. Darling Marine Center, University of Maine, Waltham, ME 04573, USA
2. Scripps Institution of Oceanography, La Jolla, CA 92032, USA
3. Biologische Anstalt Helgoland, Wattenmeerstation Sylt, D-25989 List/Sylt, Germany

Abstract
Nocturnal activity of organisms living in intertidal mud flats was previously thought to be a result of predation avoidance behaviour. However, many organisms (e.g., nemertines) which have been reported active during night low tides are known to be ignored as prey items by shorebirds.

Nemertines, like some other endobenthic predators, forage at the sediment surface. During their reproductive periods they can be observed on exposed tidal flats searching for mating partners. In this study we examined their diel and seasonal activity pattern in detail.

In laboratory experiments, the nemertine Lineus viridis appeared at the sediment surface at night, and was found in highest numbers at night low tide. On exposed tidal flats, many nemertines were active during night low tides, but none at day low tides. The nemertines L. viridis and Amphiporus lactifluus were observed only in low numbers at the sediment surface in the late summer; during their reproductive period (March and December, respectively), both nemertine species were active at the sediment surface. Immigration into mussel clumps by both nemertine species was highest during their respective reproductive periods. L. viridis foraged during nocturnal low tides in summer, and during its reproductive period (March) followed the traces of other individuals. No such behaviour, either foraging or mating, was observed for A. lactifluus.

We hypothesize that for endobenthic predators like nemertines which forage at the sediment surface, resource location via chemoreception is facilitated at low tide. Additionally prey escape is restricted during low tide. Desiccation stress, competition with fast visual predators and predation are the most important factors affecting them during diurnal low tide activity.

The role of endobenthic predators in structuring soft-bottom communities may be based on their temporal activity pattern. Non-predatory infauna facing both high epibenthic- and endobenthic predation in some areas may have to emigrate episodically or permanently.

Keywords: nemertines, endobenthic predators, diel rhythm, intertidal, chemoreception.

Introduction
Nocturnal activity of benthic organisms is a well known phenomenon in coastal areas (Enright 1975). The distinct nocturnal activity peak of the so-called demersal zooplankton in subtidal waters is thought to result primarily from predation pressure exerted by visually oriented predators (Hobson & Chess 1976, Robertson & Howard 1978, Aldredge & King 1980). Benthic organisms of many taxa participate in nocturnal ascents into the water column to feed, migrate, mate, spawn, or moult (Anger & Valentin 1976, Hammer 1981, Dauer et al. 1982, Aldredge & King 1985).

This general activity pattern is reported mostly from subtidal coastal areas. These studies are mainly concerned with differences in activity between day and night and may neglect a possible tidal influence. In intertidal areas the pattern becomes more complicated (e.g., Reid & Naylor 1989, Armonies 1989, 1992). Here many benthic organisms adapt their activity rhythm to the tidal cycle. Filter feeders are typically active during high tide (Newell 1979), while scavenging or predatory organisms appear more active during low tide (Enright 1975). Organisms which are active at low tide may face predation pressures both during day and during low tide, and thus their diel activity pattern is often very distinct. The high nocturnal activity of endobenthic organisms emerging at the sediment surface of exposed tidal flats (Dugan 1980) is thought to be an expression of predator avoidance behaviour (Vader 1964, Evans 1987).

However, some intertidal organisms, although unattractive as prey for shorebirds, are almost exclusively active during night low tides. The polychaete Anaitides mucosa, which is often active on exposed tidal flats at night (Vader 1964, Pienkowski 1983), is ignored by potential predators (Hüttem 1984). Nemertines, abundant in certain habitats, appear to have few enemies (Nordhausen 1988), because they secrete unpalatable substances (Prezant 1980, Kem 1985). In spite of this they have been observed in great numbers on exposed tidal flats during the night (Roe 1970, 1976, Thiel & Reise 1993).

This led us to hypothesize that nocturnal low tide activity of some organisms in the intertidal area may be driven by factors other than predation pressure from shorebirds. Here we summarize results on the diel and seasonal activity pattern of two intertidal nemertine species, the heteronemertine Lineus viridis and the hoplonemertine Amphiporus lactifluus. We present a possible explanation for the observed diel activity pattern. Surprisingly little is known about the behaviour of intertidal invertebrates which are active on the sediment surface during low tide. Understanding the temporal activity patterns of soft-bottom inhabitants is essential to explain their spatial distribution.

Materials and methods
The study area is located near the island of Sylt in the Wadden Sea. It consists of sandy and muddy tidal flats with an average tidal range of 1.8 m (for detailed description see Reise 1985, Thiel & Reise 1993). Mussel clumps (Mytilus edulis),
important microhabitats for nemertines in tidal flats (Thiel & Reise 1993), occur throughout the tidal flats in the study area. The tidal flats may be covered with ice-rafts during some years, but were ice-free throughout most of the winter 1991/92.

In the laboratory, day and night high and low tides were simulated in a tank with sediment (surface area 1 m²). Individuals of *Lineus viridis* (25) were introduced into the tank and they burrowed immediately into the sediment. During five days with two high and two low tide simulations per day, the number of nemertines active at the sediment surface were counted in four experimental combinations (day high tide, day low tide, night high tide and night low tide). These combinations were tested for differences using the Tukey-test (Zar 1984).

In the field, all *L. viridis* crawling on the sediment surface were counted in an area of 100 m². The study plot was observed once every low tide over a period of one month. Light intensity was measured simultaneously during each nemertine count. During night low tides a torch was used to survey the study plot. The use of the torch had no obvious influence on the nemertine behaviour at night.

In order to investigate seasonal differences in nocturnal nemertine activity at exposed tidal flats, three study plots of 100 m² were set up above the mid-tide level (Thiel 1992). In this tidal region, the nemertine abundance is highest in the intertidal region (see Thiel & Reise 1993). The three plots were surveyed over one week in each of three months (September and December 1991 and in March 1992). Due to weather conditions, not all plots could be counted every night. The number of observations for each study plot per survey month therefore varied from 5 to 7. The numbers of *L. viridis* and *Amphiporus lactiflorus* active at the sediment surface during night low tides were counted, using a torch.

The seasonal activity pattern of nemertines at the sediment surface can be studied by recording numbers of nemertines at the sediment surface during low tide. However, this gives no information regarding whether nemertines may also move during high tide or within the sediment. The preference for mussel clumps by the two nemertine species examined (Thiel & Reise 1993) enabled us to establish a simple control experiment to check the results obtained from the night observations. Nemertine-free mussel clumps were transplanted from the low tide line into an area of high nemertine abundance in the high intertidal (area size: 100 m × 200 m). The immigration of nemertines into the transplanted mussel clumps may be considered a measure of their activity. On 1 September 1991, 50 mussel clumps were transplanted, and an additional 90 clumps were transferred into the study area on 24 October 1991. Over a period of six months (1 September 1991 - 28 February 1992) ten randomly selected mussel clumps were collected every two or four weeks and examined for resident macrofauna. On 3 October 1991, 18 December 1991 and 25 February 1992, ten naturally established mussel clumps from the experimental field were collected to serve as controls.

**Results**

*Diurnal and tidal rhythm in activity of Lineus viridis*

The highest numbers of nemertines *Lineus viridis* in the experimental tank were active during night low and night high tide (Figure 1). The differences between day low tide and night low tide were significant (Tukey-test; p < 0.05), whereas differences between day high tide and night high tide were not significant (Tukey-test; p ≥ 0.05). During night low tide, more nemertines came to the sediment surface than during night high tide (Figure 1). In exposed tidal flats, *L. viridis* was never found during day low tides (Figure 2). Even at relatively low light intensities no *L. viridis* appeared at the sediment surface (Figure 2).
Seasonal rhythm in activity of nemertines

The numbers of nemertines active during night low tides differed substantially throughout the study period (Figure 3). Very few nemertines were recorded at the sediment surface during summer. In the high intertidal, the numbers of nemertines active at the sediment surface were much higher than around the mid-tide level (Figure 3).

The activity of *L. viridis* decreased from September to December (Figure 3A). The numbers of *L. viridis* drastically increased between December and March, when at times more than 100 individuals/100 m² were active at the sediment surface during night low tide. In contrast to *L. viridis*, the activity of *Amphiporus lactifloreus* increased between September and December (Figure 3B). This high nocturnal activity of *A. lactifloreus* then stayed nearly constant until March.

Almost no nemertines immigrated into the transplanted, nemertine-free, mussel clumps in autumn 1991 (Figure 4). The numbers of *L. viridis* remained low throughout autumn and early winter, then suddenly increased between January and February (Figure 4A). In contrast to *L. viridis*, the numbers of *A. lactifloreus* in the transplanted mussel clumps started to increase in December and remained high until February (Figure 4B). At the end of October 1991, significantly more *A. lactifloreus* were living in the naturally established mussel clumps than in the transplanted mussel clumps (Mann-Whitney U-test, p < 0.05).

Observations on nemertines at the sediment surface

During night low tides, the nemertines appeared at the sediment surface about 30 minutes after the tide had receded. In the first hour of tidal flat exposure, the numbers of active nemertines remained very high. Towards the end of the low tide the numbers of nemertines decreased continuously, and, shortly before the tidal flats were covered again by the incoming tide, no nemertines could be observed at the sediment surface.
During the summer, the nemertine *L. viridis* occasionally could be observed preying on *Nereis diversicolor* at night low tide. Nemertines were found to track the polychaetes on the tidal flats. Only one nemertine was found feeding on a polychaete at the surface, but several nemertines were observed to disappear into the burrows of the polychaetes, apparently in search of prey. Sometimes only the anterior end of a nemertine was in the burrow while its posterior end was still exposed at the sediment surface. When the nemertines were collected, they were found to be feeding on the polychaetes.

During the mating season in March, no *L. viridis* could be observed preying on polychaetes. Often the smaller males were attached to the larger females. Occasionally the nemertines were found to follow each other in their tracks. In the period of February/March 1992, *L. viridis* could also occasionally be seen at the sediment surface during day low tides.

*A. lactiflores* was only once observed in the field to feed on its preferred prey, the amphipod *Gammarnus locusta*. This individual was feeding on the amphipod in the algal cover of a mussel clump. The nemertines *A. lactiflores* which were observed at the sediment surface in December and March were never seen in clusters of males and females, as described above for *L. viridis*.

**Discussion**

The investigated nemertines *Lineus viridis* and *Anhiporus lactiflores* are almost exclusively active at night and show a strong preference for low tide activity. The same general activity pattern is even more striking in the nemertine *Parameristes peregrina*, which in field investigations was rarely observed at the sediment surface during high tide (Roe 1976).

**Activity of nemertines during the reproductive period**

In the study area the heteronemertine *L. viridis* starts to reproduce in late February (Bartolomaeus 1984). From our observations it is evident that the highest activity of *L. viridis* occurs during its reproductive period.

Gibson (1982) cites April through June as the reproductive period for *A. lactiflores*. Recent studies on the developmental stage of their gonads indicate however, that this species reproduces during the late fall (Thiel & Dernedde, pers. comm.). Thus, for *A. lactiflores* there may also exist an overlap between high activity on exposed tidal flats at night and the reproductive period. The same is true for the polychaete *Amphitides mucosa*, which, during its reproductive period, gathers at the sediment surface in large numbers at nocturnal low tides (Sach 1975). Despite the fact that the reproductive period of many coastal organisms, especially those in subtidal waters, is characterized by strong lunar periodicity (Enright 1975), no evidence was found for a lunar rhythm in intertidal nemertines (see also Roe 1971, 1976, 1979).

**Enhanced resource location at low tide**

It is not only the location of mating partners, but also the location of prey that is facilitated at low tide (Roe 1976, Nordhausen 1988). In particular predators and scavengers, feeding on patchy resources, rely on effective location of their food resources. Many predators and scavengers in the marine environment use chemoreception to locate their food resources (review by Atema 1988). This is true for predatory and scavenging polychaetes (Evans 1971) and nemertines (this study). Successful detection of a resource, whether a potential mating partner or a food item, depends mainly on the concentration of the chemical cues emitted by the resource. At high tide, an effective mixing in the turbulent intertidal waters makes it difficult to recognize variations in concentrations of chemical substances, (see for example Asmus et al. 1992). Under a high tide situation, even moderate current velocities may drastically decrease the foraging success of a benthic predator employing chemical senses to locate prey (Weissburg & Zimmer-Faust 1993). Under low tide conditions, the unidirectional currents and highly reduced current velocities in the thin water film remaining on the exposed tidal flats may allow the establishment of a clear chemical pattern. It is therefore concluded that resource location in the intertidal environment is much easier during low tide than it is during high tide.

The hypothesis that predators or scavengers may especially profit from facilitated food location during low tide is supported by the high proportion of this feeding guild among those organisms which are reported to be active at low tide (Table 1). In addition to facilitated prey location, predators may improve their chances of a successful encounter during low tide, as the prey cannot escape into the water column (Thiel & Reise 1993). Escape responses of prey organisms during low tide may be much less successful than during high tide (Behrends & Michaelis 1977; McDermott 1976, own obs.).
Temporal restriction to nocturnal low tide activity

Epibenthic predation, which is thought to drive selection against diurnal activity, can be neglected for nemertines and some other endobenthic predators due to their toxic secretions (see for example Prezant 1980, Kem 1985). However, for some endobenthic organisms which belong to the prey spectra of epibenthic predators, the predation pressure may very well be an important factor governing their diel activity pattern. It is not surprising therefore that predator avoidance is considered an important factor determining nocturnal activity (Vader 1964, Evans 1987). Another explanation for nocturnal low tide activity is the avoidance of desiccation stress during day low tides (Vader 1964). Nemertines and other worm-like organisms are soft-bodied and have few or no morphological mechanisms to deal with desiccation. For these soft-bodied organisms, desiccation may thus be an important factor selecting against diurnal low tide activity. Fiddler crabs and other decapods are relatively better adapted for low tide activity than are worms or other crustaceans like amphipods. Despite the fact that they are important prey for visually oriented shorebirds which prey on them more successfully during day low tides, fiddler crabs (Uca tangeri) and mudprawns (Upogeba africana) are reported to be equally or more active at day than at night low tides (Zwarts 1990, Turpie & Hockey 1993).

In contrast to subtidal areas where predation pressure seems to be the main cause of the distinct diel activity pattern, in the intertidal the importance of predation remains a matter of debate. Some studies show that low tide predation by shorebirds may drastically decrease the abundance of some intertidal organisms (Quammen 1984, Evans 1987). Even where shorebirds do not exert a significant quantitative impact on the abundance of intertidal organisms, they may affect a population of intertidal organisms qualitatively, e.g., by taking individuals which come too close to the sediment surface during the day (Boates & Smith 1989).

Some endobenthic predators follow their prey on the sediment surface over comparatively long distances before they finally overtake them (Behrends & Michaelis 1977, own obs.). During these hunts, slow endobenthic predators like polychaetes and nemertines may lose their prey to faster predators like decapods, fish, or, during low tide, birds. The only period when these slow-moving endobenthic predators enjoy reduced competition with the fast epibenthic predators, is during nocturnal low tides.

In general, the restriction to nocturnal low tide activity means that only a limited time period is available for resource location. Depending on the distribution of the considered organisms in the intertidal zone, this time period may differ significantly. Nemertines which occur in highest abundances in the upper intertidal (Thiel & Reise 1993) have more time available for resource location than organisms which live in the lower intertidal (Roe 1993). The same reason is mentioned by Emson (1977) for the occurrence of Eubalia viridis in the high rocky intertidal.

How do endobenthic predators structure soft-bottom communities?

Endobenthic predators have an important influence on the community structure in soft-bottom habitats (Ambrose 1991). Their effect on other infaunal inhabitants has to be distinguished from the effects exerted by epibenthic predators (Thiel & Reise 1993). Endobenthic predators are often referred to as intermediate predators between

<table>
<thead>
<tr>
<th>Species</th>
<th>Low tide</th>
<th>Day</th>
<th>Night</th>
<th>Feeding</th>
<th>Migrating</th>
<th>Reproduction</th>
<th>Other</th>
<th>Feeding guild</th>
<th>Main predators</th>
<th>Reported in</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hydrobia ulvae</td>
<td>+ (+)</td>
<td>+</td>
<td></td>
<td>(+)</td>
<td></td>
<td></td>
<td></td>
<td>deposit feeder</td>
<td>birds, fish, invertebr.</td>
<td>1, 6, (10)</td>
</tr>
<tr>
<td>Upogeba africana</td>
<td>+ +</td>
<td>+</td>
<td></td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td>deposit feeder</td>
<td>birds</td>
<td>13</td>
</tr>
<tr>
<td>Carcinus maenas</td>
<td>+ (+)</td>
<td>+</td>
<td></td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td>pred, scaveng.</td>
<td>birds, fish</td>
<td>8, own obs.</td>
</tr>
<tr>
<td>Uca tangeri</td>
<td>+ (+)</td>
<td>+</td>
<td></td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td>deposit feeder</td>
<td>birds</td>
<td>12</td>
</tr>
<tr>
<td>Cragon cragon</td>
<td>+ (+)</td>
<td>+</td>
<td></td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td>pred, scaveng.</td>
<td>birds, fish, invertebr.</td>
<td>1, own obs.</td>
</tr>
<tr>
<td>Gammaurus spp.</td>
<td>+ - (+)</td>
<td>+</td>
<td></td>
<td>?</td>
<td></td>
<td></td>
<td></td>
<td>detritus feeder</td>
<td>birds, fish, invertebr.</td>
<td>1, own obs.</td>
</tr>
<tr>
<td>Carcinus medota</td>
<td>- + (+)</td>
<td>- +</td>
<td></td>
<td>(+)</td>
<td></td>
<td></td>
<td></td>
<td>deposit feeder</td>
<td>birds, fish, invertebr.</td>
<td>6</td>
</tr>
<tr>
<td>Ulianura viridis</td>
<td>+ (+)</td>
<td>+</td>
<td></td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td>pred, scaveng.</td>
<td>?</td>
<td>4</td>
</tr>
<tr>
<td>Amphilomus macula</td>
<td>+ +</td>
<td>+</td>
<td></td>
<td>?</td>
<td></td>
<td></td>
<td></td>
<td>omnivore</td>
<td>birds, fish, invertebr.</td>
<td>1, 7, 8, own obs.</td>
</tr>
<tr>
<td>Haraposus maisi</td>
<td>+ - +</td>
<td>+</td>
<td></td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td>omnivore</td>
<td>birds, fish, invertebr.</td>
<td>1, 6, 10, own obs.</td>
</tr>
<tr>
<td>Neris diversicolor</td>
<td>+ - +</td>
<td>+</td>
<td></td>
<td>?</td>
<td></td>
<td></td>
<td></td>
<td>predator</td>
<td>?</td>
<td>1, (5)</td>
</tr>
<tr>
<td>Eleone longa</td>
<td>+ - (+)</td>
<td>+</td>
<td></td>
<td>(+)</td>
<td></td>
<td></td>
<td></td>
<td>predator</td>
<td>no predators</td>
<td>2</td>
</tr>
<tr>
<td>Paraventris peregrina</td>
<td>+ (+)</td>
<td>+</td>
<td></td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td>predator</td>
<td>no predators</td>
<td>3</td>
</tr>
<tr>
<td>Tetranema mutumacephalum</td>
<td>+ (+)</td>
<td>+</td>
<td></td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td>predator</td>
<td>no predators</td>
<td>9, 11, this study</td>
</tr>
<tr>
<td>Linus viridis</td>
<td>+ (+)</td>
<td>+</td>
<td></td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td>predator</td>
<td>no predators</td>
<td>this study</td>
</tr>
<tr>
<td>Amphilorus lactiflorus</td>
<td>+ - +</td>
<td>+</td>
<td></td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td>predator</td>
<td>no predators</td>
<td>this study</td>
</tr>
</tbody>
</table>

References

Table 1. Endo- and epibenthic macrofauna species from intertidal areas, which are reported to be active at low tide, at least periodically; + means that the respective behaviour is reported in the cited literature; = means that they are reported to be not active in the respective period; ? means that the respective behaviour is probable, but not reported.
epibenthic predators and the non-predatory infauna (Ambrose 1984, 1991, Comito & Ambrose 1985). We propose that one important aspect of this mediating role is the activity pattern of endobenthic predators. Some endobenthic predators may, during their activity periods, make their potential prey more susceptible to epibenthic predation, while they themselves are relatively resistant to epibenthic predation. Infaunal organisms faced with both endo- and epibenthic predation have the option to adjust either their behaviour or their distribution in response to this pressure. Emigration behaviour in soft-bottom communities is especially well reported from macrofaunal organisms which belong to the prey spectra of both epi- and endobenthic predators, such as the amphipod Corophium volutator (see Barsch 1977, Rönn et al. 1988, Boates & Smith 1989, Mouritsen 1993) or the polychaete Neris diversicolor (Zwarts & Esselink 1989, Thiél & Reise 1993). The need to avoid both epi- and endobenthic predation may also exist in subtidal waters and be partly responsible for the distinct diel vertical migrations of the so-called demersal zooplankton.

Acknowledgements
We thank G. François-Zubillaga, A. Laursen and G. Teegarden and two anonymous reviewers who gave many helpful comments on the manuscript. The participation of M. Thiél at the 28th EMBS was made possible by travel grants from the Association of Graduate Students and the Department of Oceanography at the University of Maine. This study is supported by the Federal Environmental Agency, Environmental Research Plan of the Ministry for the Environment, Nature Conservation and Nuclear Safety of the Federal Republic of Germany (Grant 02 02 085/01), by the state of Schleswig-Holstein, and by the National Science Foundation Grant No. OCE 9206834. This is publication No. 139 of the project Ecosystem Research Wadden Sea.

References
Piernkowski, M.W., 1983. Surfacing activity of some intertidal invertebrates in relation to temperature and the
Prezant, R.S., 1980. An antipredation mechanism of the polychaete Phtyloba mucoa with notes on similar
Quannen, M.L., 1984. Predation by shorebirds, fish, and crabs on invertebrates in intertidal mud flats: an
Reid, D.C. & E. Naylor, 1989. Are there separate circatidal and circadian clocks in the shore crab Carcinus mac-
Roe, P., 1970. The nutrition of Pararanemertes peregirina (Rhynchocuca: Hoplonemertea). I. Studies on food and
Roe, P., 1971. Life history and predator-prey interactions of the nemertean Pararanemertes peregirina Coe. -
Bull. 150: 80-106.
Roe, P., 1993. Aspects of the biology of Pantinnotremes californiensis, a high intertidal nemertean. - Hydro-
biologia 266: 29-44.
Rönn, C., E. Bonsdorff & W.G. Nelson, 1988. Predation as a mechanism of interference within infauna in shal-
low brackish water soft bottoms: experiments with an infauna predator, Nereis diversicolor O.F. Müller. -
172.
of premigratory grey plovers Pluvialis squatarola and whimbrels Numenius phaeopus in South Africa. - Ibis
135: 156-165.
Vanden, W.T.M., 1964. A preliminary investigation into the reactions of the infauna of the tidal flats to tidal
Zwarts, L., 1990. Increased prey availability drives premigration hyperphagia in whimbrels and allows them
to leave the Banc d'Arguin, Mauritania, in time. - Ardea 78: 279-300.