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Nemertines as predators on tidal flats – High Noon at low tide

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Abstract

Nemertines can be important predators on tidal flats. They have been found to be preferentially active at night low tides. To understand the role of these (and other) predators, it is important to understand how they find their prey on tidal flats. Field observations revealed that the nemertine *Lineus viridis* feeds on post-spawn *Nereis virens* in the spring. Field experiments demonstrated that the placement of post-spawn or freeze-thawed *N. virens* on tidal flats can elicit a foraging response of *L. viridis*. Nemertines came to the sediment surface in large numbers and crawled toward the prey. Comparative experiments showed that more nemertines were attracted to the sediment surface at day low tides than at day high tides. More nemertines were attracted at night low tides than at day low tides. Numbers of active nemertines on tidal flat areas without prey were always much lower than on tidal flat areas with prey. In an experimental flume in the laboratory, starved nemertines were attracted to prey at current velocities of about 2 cm s^{-1}. Regardless of whether it was a simulated high tide or low tide in the flume, successful nemertines required about 30 min to cover a distance of 50 cm between the starting point and the prey. It is concluded that the high activity of nemertines during night low tides is due in part to the enhanced probability of locating prey, but is also influenced by prey behavior and potential competitors. Predatory nemertines such as *L. viridis* easily cover relatively large distances of 5–10 m in the field, and may thus effectively influence the small-scale distribution of their potential prey on tidal flats. It is proposed to take the activity pattern, mobility and foraging range of predators into account when examining their role in marine soft-bottom assemblages.

Introduction

Predators play an important role in marine soft-bottom assemblages (e.g. Commito & Ambrose, 1985; Ambrose, 1991). They are often categorized as either being epibenthic (above-bottom) or endobenthic (within-bottom) predators, yet this categorization not always proves satisfactorily. Many predators frequently switch between epi- and endobenthic life-style. Decapod crabs, many of which are considered epibenthic predators, often bury within the sediment for long time periods, and many nemertine which are considered endobenthic pursue their prey along the sediment surface (Nordhausen, 1988; Kruse, 1996). The analysis of predator-prey interactions in marine soft-bottoms based on this categorization in epi- and endobenthic predators has led to a very controversial discussion of the roles of these two predator categories (Ambrose, 1984, 1986; Wilson, 1986). I suspect that the explanatory power of this analysis is hampered by the fact that the distinction of epi- and endobenthic predators does not provide sufficient information to determine the role of these respective predators. Very little attention has been devoted to the behavior of predators in marine soft-bottoms. Hardly anything is known about the proportions of predators actively foraging, their foraging speeds, their foraging range and the factors determining the foraging success of predators. This knowledge, however, is probably essential to understand the roles of different predators in marine soft-bottoms.

Many marine predators or scavengers rely on chemoreception (Roe, 1971, 1976; Hüttel, 1984; Crisp, 1969, 1978). Recent investigations of the chemoreceptive capabilities of benthic predators primarily focused on fast ‘epibenthic’ predators such as decapod crabs (Zimmer-Faust et al., 1988; Zimmer-

Faust, 1989; Atema, 1988; Weissburg & Zimmer-Faust, 1993). These predators have wide foraging ranges (Wolcott & Hines, 1989), and their presence at a certain location is relatively unpredictable. The presence or absence of 'endobenthic' predators, on the other hand, seems to be relatively predictable, and this may be important in determining the attractiveness of a locality to potential settlers (see e.g. Armonies, 1994). However, not only the presence of an endobenthic predator is of relevance for a potential prey organism but also its activity pattern. We recently speculated on the possibility that high activity of endobenthic predators may induce an emigration response of other soft-bottom organisms (Thiel et al., 1995). Armonies (1989, 1994) indicated that benthic predation may be one cause for emergence of meiobenthic organisms into the water column at night.

In order to address these issues, I examined the foraging behavior of a typical soft-bottom predator, the nemertine *Lineus viridis.* It was chosen, because nemertines are important predators (Ambrose, 1991), and they can be relatively easy observed (see e.g. Roe, 1971, 1976; Nordhausen, 1988). Many nemertine species and high nemertine abundances are reported from intertidal soft-bottom environments (Reise, 1985; Nordhausen, 1988; Roe, 1993; Thiel & Reise, 1993). In this habitat, the nemertines are preferentially active at low tides (Roe, 1971, 1976, 1979), and often exclusively so at night low tides (Nordhausen, 1987; Thiel, 1992; Thiel et al., 1995). This distinct activity rhythm may be due to the fact that prey escape in the intertidal area is largely restricted during low tide (McDermott, 1976; Thiel & Reise, 1993; Armonies, 1994). In addition, during low tide, the resource location may be facilitated for these relatively sluggish predators (Thiel et al., 1995).

The major goals of this study were to determine the factors influencing the foraging success of *L. viridis* and the foraging speeds of this nemertine. Prey items were placed on the tidal flats at different tidal and diel stages to examine under which conditions nemertines successfully locate their prey. Experimental manipulations, in which only the tidal level was varied, were carried out in the lab in order to examine the influence of the tidal level on the chemoreceptive abilities of nemertines.

Material and methods

Study area

All field experiments were carried out on the tidal flats of Lowes Cove, Damariscotta River, Maine (Figure 1). The tidal range in the Damariscotta River is about 3.0 m, and the average salinity is about 30‰. The sediments consist of sandy muds. In Lowes Cove, one central gully drains several small freshwater streams during low tide. Small creeks on the tidal flats, which are about 10–20 cm wide and carry about 0.5 cm deep water throughout the low tide period, drain the remaining water from the tidal flats into the central gully. These creeks are a regular feature of the tidal flats in Lowes Cove unless the tidal flats are dug up by clam diggers or covered by green algae. They are often in proximity and run more or less parallel to each other. The distance between two of these tidal creeks rarely exceeds 4 m. Most field experiments were undertaken in these tidal creeks.

Nemertines and prey

The nemertine *Lineus viridis* is a common predator in coastal areas worldwide (Gibson, 1972, 1982). *L. viridis* pursues its preferred prey, the polychaete *Nereis diversicolor*, along mucus trails made by the prey, overtaking it on the sediment surface or in its burrow. In the intertidal zone, the nemertine *L. viridis* forages preferentially during nocturnal low tides (Reise, 1985; Nordhausen, 1987, 1988; Thiel, 1992; Thiel et al., 1995).

During spring 1993, nemertines were frequently observed feeding on post-spawn *Nereis virens* that remained on tidal flats after the tide receded. These post-spawn polychaetes were collected and placed in the above described small creeks on the tidal flats of Lowes Cove to attract nemertines. Later in the season, when post-spawn *N. virens* became rare, freeze-thawed polychaetes were used instead. Both types of available prey items attracted nemertines *L. viridis* in field and laboratory experiments, but freeze-thawed *N. virens* proved significantly more attractive than post-spawn *N. virens* (Mann-Whitney *U*-test, $p < 0.05$).

Field experiments

The field experiments were undertaken between 25 May 1993 and 16 June 1993 in Lowes Cove. One prey item each (ps = post-spawn, or ft = freeze-thawed

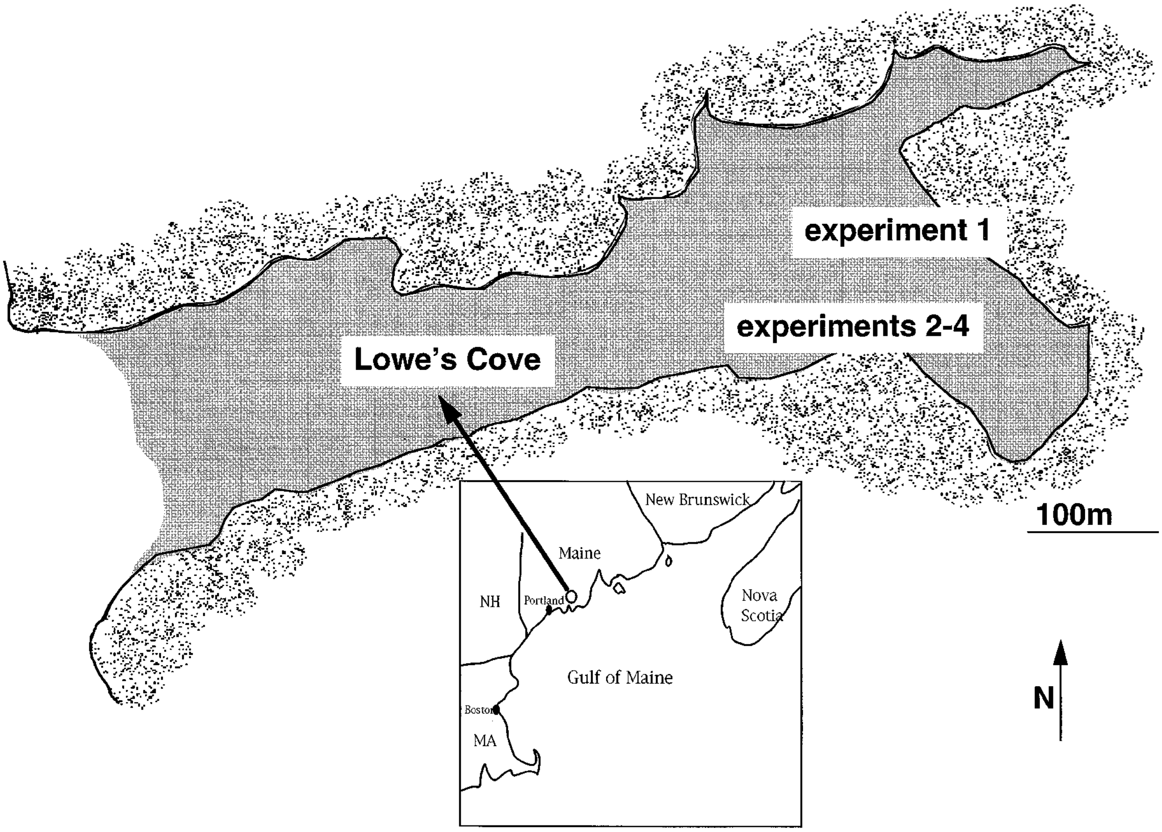

Figure 1. The study area in Lowes Cove, Damariscotta River, Maine; all experiments were carried out on the tidal flats (gray shading) in the eastern part of the Cove.

Nereis virens) was placed in the small creeks. All *Lineus viridis*, which were attracted to the sediment surface in these small creeks, were counted within 5 m downstream from the prey items. In all experiments prey were left exposed for 2 h, and at the end of the experiment the prey were collected together with the nemertines that had reached the prey. For each experiment two different treatment conditions were compared simultaneously (e.g. 'day low tide versus night low tide' or 'day low tide versus day high tide'). For each experiment 12 tidal creeks were chosen in one area, six of which were selected randomly for each treatment. Each tidal creek was only used once, as nemertines were taken away from the creeks after the experiments. A flashlight, which was used for nocturnal counts, had no visible influence on the behavior of the nemertines.

Experiment 1: DLT-DHT : ps-prey is the comparison 'day low tide versus day high tide' with post-spawn prey, carried out to determine whether more nemertines are attracted to the sediment surface and reach the prey during low tide than during high tide. Nemertine numbers in six creeks (5 m downstream from prey) were counted every 20 min during day low tide (DLT), and every 40 min in six other creeks during day high tide (DHT). During day high tide, I snorkeled 5 m downstream from the prey counting all nemertines at the sediment surface along the creek transect. At the end of the experiment (after 2 h of prey exposure) nemertines that had reached the prey items were collected and counted. The experimental creeks were located on the east side of Lowes Cove (Figure 1).

Experiment 2: DLT-NLT : ps-prey is the comparison 'day low tide versus night low tide' with post-spawn prey, carried out to determine whether more nemertines are attracted to the sediment surface and reach the prey at night low tide than at day low tide. Nemertine numbers in six creeks (5 m downstream from prey) were counted every 20 min during day low tide (DLT), and in six other creeks during night low tide (NLT). At the end of the experiment (after 2 h of prey exposure), nemertines that had reached the prey items were collected and counted. The experimental creeks were located on the south side of Lowes Cove (Figure 1).

Experiment 3: DLT-NLT : no-prey is the comparison 'day low tide versus night low tide' without prey, carried out to determine whether nemertines are preferentially active at night low tides. Nemertine numbers in six creeks (5 m length per creek) were counted during day low tide and during the following night low tide in the same creeks. The experimental creeks were on the south side of Lowes Cove (Figure 1).

Experiments 1–3 are comparable only within the experimental treatments, but not within the different experiments, as the experiment 1 was done under different conditions and in different localities than experiments 2 and 3. The Mann-Whitney U-test was used to test for significant differences between experimental treatments (Zar, 1984).

Experiment 4: DHT-DLT-NHT-NLT : ft-prey was carried out with freeze-thawed prey to determine the natural conditions under which more nemertines successfully reach the prey. Freeze-thawed polychaetes *Nereis virens* were exposed in an area of about 50 m^2 at 24 locations ($n = 6$ locations for each treatment DHT, DLT, NHT, NLT), which were randomly selected before the experiment started. Prey were left exposed in mesh bags for 4.5 h during low tides and 6 h during high tides. Nights were too short during the time of the experiment (9–16 June 1993) to cover a complete low and a complete high tide cycle. The high tide portion of the experiment was therefore done on 9 June and the low tide portion on 15–16 June. As soon as the mesh bags were exposed again after a high tide treatment, or just before they were submerged again after a low tide treatment, they were collected together with the first 2 cm of sediment beneath the mesh bags. Nemertines which had reached the prey in the mesh bags were collected and counted. The number of nemertines which had reached each prey per hour was calculated. This experiment was also done in the southern part of Lowes Cove (Figure 1).

Laboratory experiments

The influence of changes in tidal height on the chemoreceptive abilities of nemertines was examined in a laboratory flume. The flume was 5 m in length, 30 cm wide and 30 cm high. The inflow chamber was 10 cm in length and outflow occurs through pores with a diameter of 1 cm (30 pores over the cross-sectional area of 900 cm^2). The experimental section was 3 m downstream from the inflow chamber and is 50 cm long. The current velocity was determined by collecting water at the outflow and calculating the average flux through the respective cross-sectional area (thus neglecting any boundary layer effects). The water level in the flume was about 0.5 cm during low tide conditions and about 25 cm during high tide conditions. The inflow was adjusted so that a current velocity of about 2 cm s^{-1} was maintained throughout each experimental treatment. The bottom of the flume was covered with sand which was exchanged after each experimental treatment. The prey (freeze-thawed *Nereis virens*) was positioned 3 m downstream from the inflow and during each experimental treatment 10 nemertines *Lineus viridis* were released 0.5 m downstream from the prey. Nemertines were observed for 60 min under a red light that had no visible influence on the behavior of the nemertines. The arrival times of nemertines that reached the prey within 60 min was noted. Nemertines were not removed from the prey during an experimental treatment. After one treatment (e.g. high tide), the sand in the flume was changed, and the corresponding second treatment (low tide) was run immediately. The sequence of the experimental treatments (high tide, low tide) per experiment was chosen by chance. For those experiments in which at least three nemertines per treatment reached the prey, the arrival times of the first three nemertines were taken for statistical analysis. Arrival times of all experiments were pooled, and a *t*-test (Zar, 1984) was used to test whether nemertines reached the prey faster under low tide conditions than under high tide conditions. Over a period of ten days in September 1993 one experiment was run each morning between 5.30 am and 8.00 am, when the laboratory was in complete darkness.

In a modified version of this experiment a trail was laid with the freeze-thawed polychaete from the starting point to the prey site. Nemertines were then introduced to the starting point under high tide conditions with a current and under low tide conditions with only a thin water film and no current. Nemertines were starved for about one week before they were used in the experiments, and every nemertine was only used once.

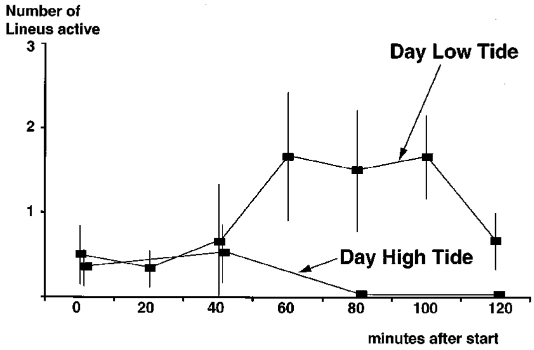

Figure 2. Average number (± standard error) of nemertines *Lineus viridis* attracted to the sediment surface in creek segments of 5 m length under Day Low Tide and Day High Tide conditions. Prey were placed on the upstream end of the stream segment. Numbers of nemertines were monitored in the creek segments for 2 h after the placement of the prey. For each treatment (Day Low Tide and Day High Tide) six individual creeks were selected. Prey items were post-spawn *Nereis virens*.

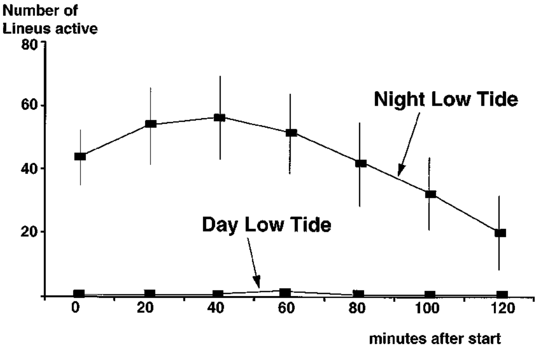

Figure 4. Average number (± standard error) of nemertines *Lineus viridis* active at the sediment surface in creek segments of 5 m length under Day Low Tide and Night Low Tide conditions. No prey were offered in this experiment. Number of nemertines were monitored in the creek segments for 2 h. For each treatment (Day Low Tide and Night Low Tide) six individual creeks were selected.

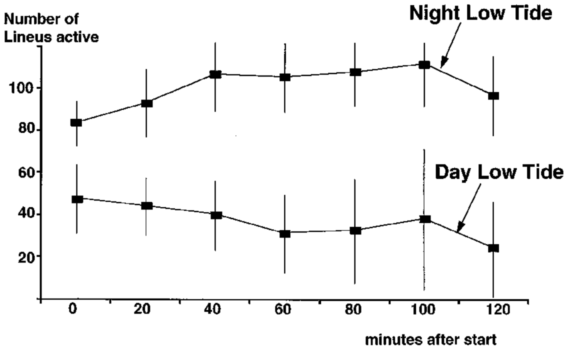

Figure 3. Average number (± standard error) of nemertines *Lineus viridis* attracted to the sediment surface in creek segments of 5 m length under Day Low Tide and Night Low Tide conditions. Prey were placed on the upstream end of the stream segment. Numbers of nemertines were monitored in the creek segments for 2 h after the placement of the prey. For each treatment (Day Low Tide and Night Low Tide) six individual creeks were selected. Prey items were post-spawn *Nereis virens*.

Results

Nemertine activity at high and low tide

The abundance of *Lineus viridis* on the east side of Lowes Cove was much lower than on the south side. The average numbers of nemertines active at the sediment surface of the tidal creeks on the east side was therefore relatively low. During day low tide, as many as 9 nemertines could be observed simultaneously in one 5 m-long creek segment, whereas at day high tide a maximum of 2 nemertines was seen only once. During the first hour of prey exposure, nemertines were active in very low numbers at both, low and high tide. After an hour, when the chemical cues released by the prey had spread over a larger area, more nemertines appeared at the sediment surface under low tide conditions, whereas nemertines under high tide conditions disappeared (Figure 2). No nemertines could be seen during the second hour of the high tide experiments. At the end of the experiment no nemertines had reached the prey during high tide. Significantly more nemertines (1.5 nemertines creek^{-1}) had reached the prey during the low tide experiment (Mann-Whitney U-test, $p < 0.05$; one-tailed). Nemertines moved directly toward the prey during low tide, whereas they did not seem to be able to locate the direction of the prey signal during high tide.

Nemertine activity at low tide with prey

Downstream from the prey, large numbers of nemertines became active at the sediment surface on the south side of Lowes Cove (Figure 3). When a prey signal was offered in the tidal creeks, nemertines came to the surface even during day low tide and moved rapidly toward the prey (Figure 3). During night low tides the average number of nemertines creek^{-1} was about 100 nemertines per 5m-creek-segment^{-1} during the entire experimental period of 2 h. No decrease in nemertine numbers toward the end of the low tide period was discernible. Although the numbers of nemertines during night low tide was constantly higher than during day low tide, there was no signifi-

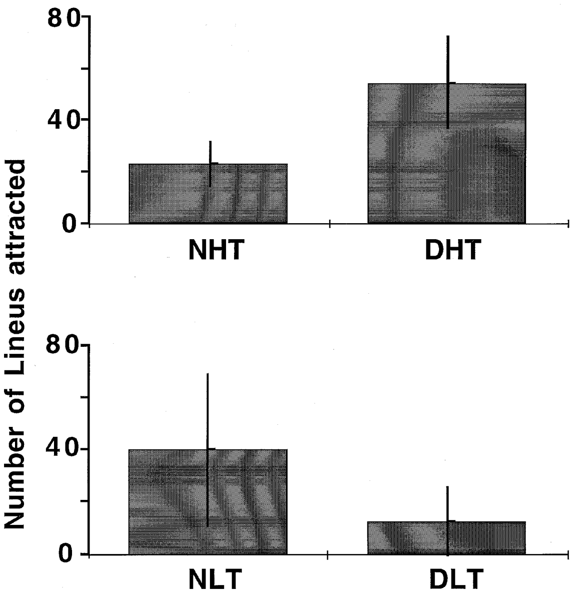

Figure 5. Average number (± standard deviation) of nemertines *Lineus viridis* attracted to the prey h^{-1} under Night High Tide and Day High Tide (9 June), and Night Low Tide and Day Low Tide conditions (15–16 June). Prey were exposed for 4.5 h during low tides and 6 h during high tides. Prey items were freeze-thawed *Nereis virens*. The experiment was carried out on the tidal flats.

cant difference in the numbers of nemertines reaching the prey between the two treatments (Mann-Whitney *U*-test, $p = 0.05$). All nemertines in the creek moved steadily upstream toward the prey. No nemertines were attracted to the prey from upstream.

Nemertine activity at low tide without prey

When no prey was offered, only one *Lineus viridis* was seen active at the sediment surface during day low tide, whereas during night low tides up to 105 nemertines creek^{-1} could be observed. An average of about 50 nemertines creek^{-1}were active at the sediment surface during night low tide (Figure 4). Toward the end of the night low tide period, the nemertines disappeared in the sediment and consequently the activity decreased continuously. The nemertines that were at the sediment surface in the creeks during night low tides moved only randomly and did not cover large distances.

Nemertines find prey at high tide and at low tide

Lineus viridis came in large numbers to the prey during day high tide and during night low tide (Figure 5). The average number of nemertines reaching the prey varied between 2.5 nemertines h^{-1} and about 8.8 nemertines h^{-1}. During the day many nemertines successfully located the prey at high tide (Figure 5a). In contrast, during the night more nemertines reached the prey at low tide than at high tide (Figure 5b).

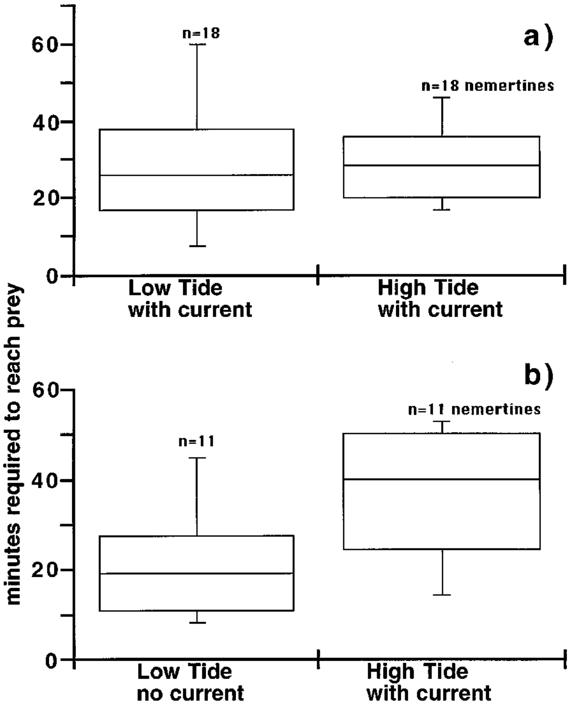

Figure 6. Time required by successful nemertines *Lineus viridis* to reach prey (freeze-thawed *Nereis virens*) in the laboratory flume; presented is the median, boxes contain 50% of the values, whiskers comprise the remaining values; dots represent outliers. Distance between starting point and prey was 50 cm. The flume was covered with sand, the current speed under both treatment conditions (low tide and high tide) was 2 cm s^{-1} in a), no current was running in the low tide treatment in b). In b) a trail with the freeze-thawed polychaete *N. virens* was laid between the starting point and the prey site. Experiments were carried out under red light.

Prey location by Lineus viridis under high and low tide simulation

Nemertines did not locate the prey faster under low tide conditions (*t*-test, $p \geq 0.05$). The first 3 nemertines which reached the prey required on average about 30 min for a distance of 50 cm between the starting point and the prey site (representing an average speed of about 1.7 cm min^{-1}) under both conditions (see Figure 6a). Four experiments had to be rejected for statistical examination because fewer than 3 nemertines reached the prey within 1 h in one of the two experimental treatments. However, in every treatment at least one nemertine successfully reached the prey. The maximum number of nemertines reaching the prey within 1 h was 8 (out of 10) in one low tide treatment.

After their introduction into the flume most nemertines disappeared in the sediment. They remained there for a few minutes until they slowly reappeared at the sediment surface and started moving toward the prey. At the end of the experiments most nemertines were found upstream from the release site, but some also moved downstream or stayed in the sediment at the starting point. When a trail was present, the nemertines reached the prey significantly faster under low tide conditions (no current) than under high tide conditions with a current of about 2 cm s^{-1} (*t*-test, $p < 0.05$) (Figure 6b).

Discussion

The offered prey items (post-spawn or freeze-thawed *Nereis virens*) were highly attractive to *Lineus viridis* in field and laboratory experiments. Nemertines were able to locate their prey over distances ranging from 0.5 m in the laboratory experiments to more than 5 m in the field. Nocturnal low tide is the most preferred activity period, but nemertines also reached their prey in considerable numbers during day high tide. The experiments revealed that chemical cues are the most important signals for this surface-foraging predator. The factors governing the transport of these cues along the sediment surface are thus of major importance for the foraging success of these nemertines.

Foraging activity of endobenthic predators in the intertidal area

Predators in most environments are thought to be only occasionally satiated. This assumption is supported by the increased initial food intake rates of endobenthic predators immediately after their transfer into the laboratory (McDermott, 1984, 1993) and by the large proportion of individuals with empty guts when collected in the field (Schubert & Reise, 1986). The food intake rate of nemertines in the laboratory slows down drastically after a few days when they are provided with a continuous food supply (McDermott, 1984, 1993; Thiel, 1992). The immediate appearance of nemertines at the sediment surface during the field experiments in Lowes Cove indicates that they were very hungry. There was no distinct preference for a certain time of day or tidal level when a strong prey signal was provided. Nemertines became active as soon as a promising food resource signaled its presence. Nemertines usually prefer to be active at night low tide (Roe, 1970, 1976; Reise, 1985; Nordhausen, 1987; Thiel, 1992; Thiel et al., 1995), and *L. viridis* showed this preference in Lowes Cove (see Figure 4). When offered a prey signal, nemertines reached the prey not only at night low tide, but also at day low tide or high tide conditions.

The preference for night low tide by nemertines may therefore not be due to an easier location of prey during these conditions, but rather to a higher probability of encountering prey on the tidal flats during night low tide compared to, e.g., day low tide or high tide. A strong and continuous prey signal, as artificially produced in the experiments, indicates a high probability that food satisfaction can be achieved, and may therefore stimulate activity under any tidal and diel condition.

Foraging success of endobenthic predators in the intertidal area

An encounter with a prey organism may be more successful during low tide than during high tide, as the escape of prey is largely restricted during low tide (Roe, 1971, 1976; McDermott, 1976; Thiel & Reise, 1993; Armonies, 1994). However, not only the success during an encounter may be increased at low tide, but also the finding of a food resource. Predators, which forage along the sediment surface depend often on chemoreception to locate their prey. Scavengers, which also rely on chemoreception, supposedly profit from being active at low tide (Hüttel, 1984; Thiel et al., 1995).

Lineus viridis appears to be stimulated by chemical cues under all diel and tidal conditions. However, in the field experiments in the creeks, no nemertines located prey when the signals were diluted over a larger area (i.e. at high tide), indicating that they are more successful under low tide conditions. In experiment 4, almost the same number of nemertines reached prey during day high tide and night low tide, which seems to contradict the above statement. The latter experiment was done in an area with a very high nemertine abundance and thus the distances covered by the nemertines were relatively small. During the high tide treatments, which were run 6 days before the low tide treatments, a significant portion of the original nemertine stock in the area may have been removed from the experimental site. It therefore cannot be concluded that the different treatments are truly independent.

The laboratory experiments also support the notion that tidal level may be of minor importance for a successful prey location by *Lineus viridis*, as nemertines reached the prey both under high and under low tide conditions. Flow in the experimental compartment of the flume was laminar, which may not reflect the natural situation in the intertidal area. Particularly in shallow water on the tidal flats, wave-action and bottom geography exert a large influence on the current regime, creating turbulent flow with continuously varying flow directions. It can therefore be assumed that the main factor governing a successful prey location by nemertines in the intertidal area is not the water level but the flow regime (laminar or turbulent flow). Nemertines cover similar distances and reach similar speeds during their foraging activity as such epibenthic predators as whelks (*Buccinum undatum*, L.) and asteroids (*Leptasterias polaris*) (Himmelman, 1988; Rochette et al., 1994). These relatively sluggish predators which forage along the sediment surface may require a relatively steady flow environment to successfully locate their prey. On tidal flats, the constantly changing current directions and the varying tidal levels may be important parameters controlling chemoreception along the sediment surface. Here the most favorable conditions for locating prey may be present during low tide, when a steady unidirectional flow of water continuously drains the tidal flats. However, for *L. viridis* chemoreception does not seem to be easier under low tide conditions than under high tide conditions. It is therefore necessary to consider other explanations for the fact that the nemertine predator *Lineus viridis* is preferentially active at night low tides. Other 'epibenthic' predators that use chemoreception, such as decapods or fish, may reach a potential prey item during high tide much faster than nemertines (see e.g. Zimmer-Faust et al., 1988; Zimmer-Faust, 1989; Weissburg & Zimmer-Faust, 1993). Decapod crabs, for example, locate prey over distances of one meter within time periods of less than a minute regardless of the flow speed (Weissburg & Zimmer-Faust, 1993). The preference for nocturnal activity by nemertines may be due in part to desiccation risk during day low tides. Another reason for the nocturnal activity of sluggish 'endobenthic' predators such as nemertines may be reduced competition with fast visual epibenthic predators such as gulls. During day low tides, prey may be removed from the exposed tidal flats by gulls and other shorebirds too quickly to constitute a potential food resource for nemertines or other 'endobenthic' predators.

Nemertines as predators and the importance of their foraging behavior

Nemertines belong to the most abundant predators in some intertidal areas (Roe, 1970, 1976; Reise, 1985; McDermott, 1988; Nordhausen, 1988; Rowell & Woo, 1990; Heine et al., 1991; Ambrose, 1991; Thiel & Reise, 1993). In areas, where they are abundant, they may prey intensively so that their prey organisms substantially decrease in numbers (Ambrose, 1991). The presence of nemertines may also cause emigration of their prey organisms (Thiel & Reise, 1993; Kruse, 1996), as is known for other endobenthic predators and their potential prey (Ambrose, 1984; Olafsson & Persson, 1986; Rönn et al., 1988; Armonies, 1994). Endobenthic organisms may have their activity periods in times when predators are inactive or ineffective in locating prey. High nocturnal activity of some benthic organisms is thought to be an effective adaptation against predation by visual predators. All of these behavioral adaptations, however, are not very effective in reducing predation pressure from 'endobenthic' predators, which often have only limited mobilities and foraging ranges and remain for long time periods in the same habitat as their prey organisms.

The comparison of the mobility and the foraging range of nemertines with those of some 'epibenthic' predators such as asteroids, whelks or decapod crabs, show that nemertines may occupy an intermediate position on this scale (see also Figure 7). They pursue their prey over relatively large distances (e.g. several m) which also was occasionally reported for predatory endobenthic polychaetes (Evans, 1971; Behrends & Michaelis, 1977). The distinction between endo- and epibenthic predators proves difficult in some of the above cases. For example, nemertines usually are considered endobenthic, but during their foraging periods they clearly assume an epibenthic life-style. Mud whelks and other gastropods are commonly classified as epibenthic, but remain buried in the sediment (= endobenthic) for extended time periods, and even such 'epibenthic' predators as decapods and fish often seek shelter in the sediment during periods of inactivity. These difficulties in categorizing predators may be the main reason why the roles of epibenthic or endobenthic predators in structuring soft-bottom assemblages could not clearly be distinguished in the past (see e.g. Ambrose, 1986; Wilson, 1986). I propose to scale

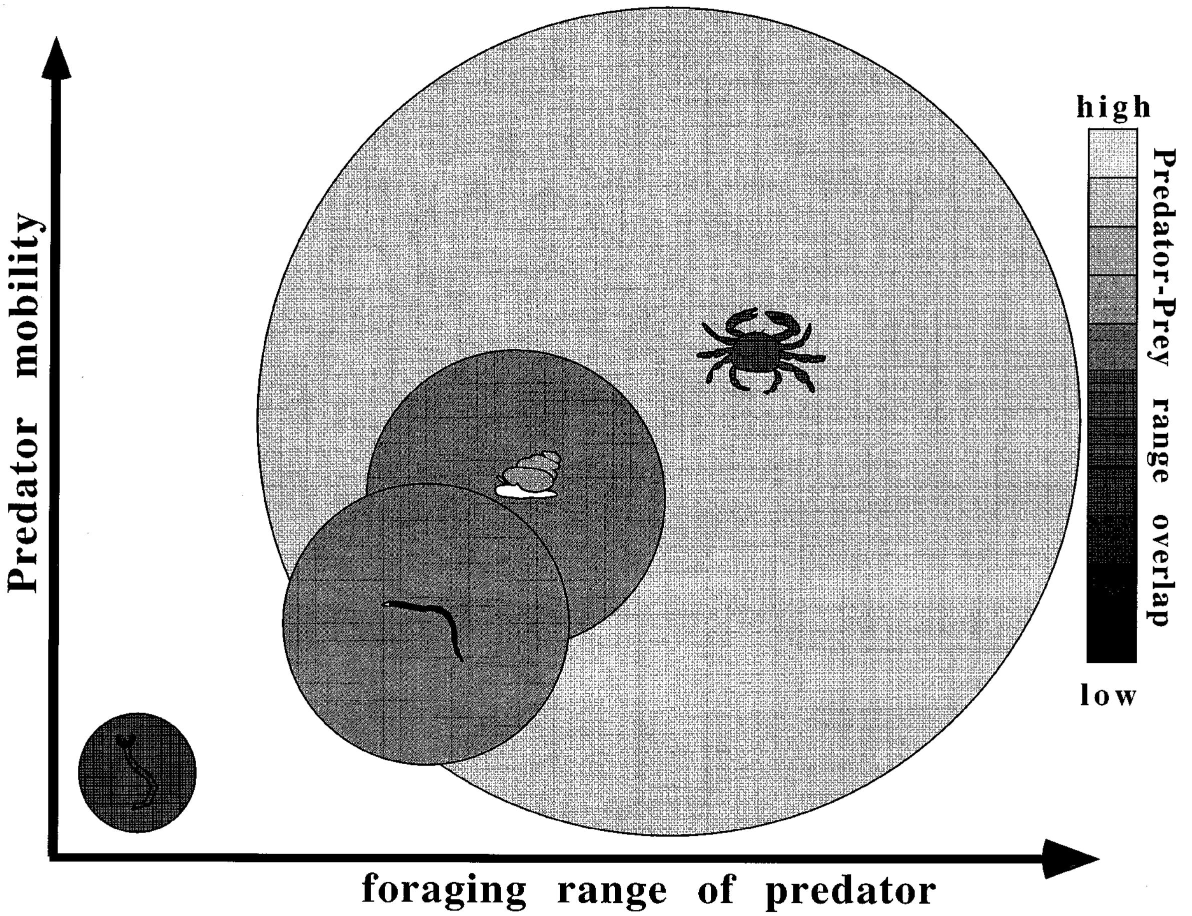

Figure 7. Exemplified mobility and foraging range of ‘endobenthic’ polychaetes, nemertines, and ‘epibenthic’ gastropods and decapods. Different mobilities and foraging ranges result in different range overlaps between predator and prey.

predators according to their respective mobilities and foraging ranges (see Figure 7), rather than trying to categorize them as endo- or epibenthic predators. A thorough understanding of their role in marine soft-bottom assemblages can only be achieved if we examine not only their abundances, but also their activity pattern, mobility, and foraging ranges.

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