INTERACTION OF NEMERTINES AND THEIR PREY ON TIDAL FLATS

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ABSTRACT

Two common nemertines of the European Wadden Sea, Lineus viridis and Amphiporus lactifloreus, occur preferentially in clusters of mussels, spread over sedimentary flats in the upper intertidal near the island of Sylt. The heteronemerine L. viridis preys mainly on the polychaete Nereis diversicolor. The hoplonemertine A. lactifloreus feeds almost exclusively on the amphipod Gammarus locusta. Abundance of both predators and their respective prey in the field showed inverse relationships.

Experimentally increased numbers of L. viridis in clusters of mussels caused a gradual decrease of nereid abundance in the sediment underneath over a period of 1 month, suggesting that losses of individuals were caused by prey capture. Experimentally increased numbers of A. lactifloreus were followed by an escape response of gammarids from clusters of mussels within 2 d. In aquaria, both prey species exhibited prolonged swimming activity when their respective predators lurked at the bottom. We conclude that escape behaviour in N. diversicolor may be only effective during its migrant phases, while G. locusta is permanently on the alert to avoid encounters with its predator. This refuging behaviour in response to endobenthic predators has strong implications on prey distribution, while the actual consumption of prey may be relatively modest. Enclosure experiments in the field and in aquaria lead to overestimates of prey capture when refuging behaviour is not accounted for.

1. INTRODUCTION

In tidal areas predators are an important factor structuring the benthic community. Most epibenthic predators invade the tidal zone intermittently, e.g. crabs and fishes during high tide (REISE, 1977, 1978; PETERSON, 1979) or birds during low tide (GOSS-CUSTARD et al., 1977). Endobenthic predators, on the other hand, stay within a certain area permanently. Although some endobenthic predators occasionally leave the sediment for feeding they often return to the same dwelling (OCKELMANN & VAHL, 1970; GOERKE, 1971; ROE, 1971; MIRON et al., 1991). As a result of a predator's foraging activity low numbers of its prey can be expected in its range (see SUMMERSON & PETERSON, 1984). Past investigations have often yielded distinct distribution patterns with inverse relationships between predator and prey numbers (REISE, 1977; OLAFSSON & PERSSON, 1986; BEUKEMA, 1987). Predator enclosures have been used to highlight the predatory impact on the prey (REISE, 1978, 1979; COMMITO, 1982; AMBROSE, 1984a, 1984b, 1984c, 1986, 1991; SCHUBERT & REISE, 1986; NORDHAUSEN, 1988; RÖNN et al., 1988; MATTILA et al., 1990). A decrease in prey abundances in these experiments may lead to an overestimate of prey capture (1) because prey species may have emigrated through wide meshes in an attempt to avoid their predators or (2) because prey species were prevented from escape by narrow meshes. This prompted us to investigate escape behaviour of prey in response to two endobenthic predators, the nemertines Lineus viridis (O.F. Müller) and Amphiporus lactifloreus (Johnston).

Nemertines are considered relatively sluggish predators (MRÁZEK, 1903; NAWITZKI, 1931; VON FRANKENBERG, 1937) with a low metabolism permitting survival for months without food (MCINTOSH, 1874; CHILD, 1901; REISINGER, 1926). These considerations seem to be contradicted by recently determined high feeding rates for some nemertine species (ROE, 1971, 1976; MCDERMOTT, 1976a, 1988; BARTSCH, 1973; NORDHAUSEN, 1987, 1988). MCDERMOTT (1984), however, found in long-term laboratory experiments an enormous initial food intake followed by a marked drop to very low feeding rates after some days. As predator avoidance behaviour in the marine benthos is mentioned by many authors (WITTE & DE WILDE, 1979; COMMITO, 1982; PETERSON et al., 1982; AMBROSE, 1984d; COMMITO & AMBROSE, 1985a, 1985b; OLAFSSON & PERSSON, 1986; RÖNN et al., 1988), we con-

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sider it likely that experimental designs interfered with the escape behaviour of prey organisms and made possible a capture rate not to be achieved by nemertines under natural conditions. Various reviews point to cage artifacts, *e.g.* water current effects, algal growth, shading effects, attraction of animals to the cages, etc. (see VJRNSTEIN, 1978; PETERSON, 1979; HULBERG & OLIVER, 1980; ARNTZ, 1981; REISE, 1985a), but mostly neglect the fact that caged animals are restricted in their movements. Physical confinement ignores the prey's susceptibility to predators and potential escape capabilities, increasing a predator's probability of encounter, attack and success. In order to avoid physical confinement we designed our field experiments on the interaction of nemertines and their prey without using cages.

The two nemertines capture their prey by rapidly evertting their proboscis and secreting or injecting substances which immediately paralyse the prey (GIBSON, 1972). The heteronemertine *L. viridis* is known to feed preferentially on the polychaete *Nereis diversicolor* (O.F. MÜLLER) (GONTCHAROFF, 1948; JENNINGS & GIBSON, 1969; NORDHAUSEN, 1988). The hoplonemertine *A. lactiflorus* preys almost exclusively on the amphipod *Gammarus locusta* (L.) (BRUNBERG, 1964; JENNINGS & GIBSON, 1969; MCDERMOTT & ROE, 1985). Both nemertines are considered endobenthic as they live mainly in the sediment and forage in a narrow range in contrast to most epibenthic predators.

Although both nemertine species occur in most coastal areas of Northern Europe, little is known about their habitat requirements. Therefore quantitative samples were taken along transects between high and low tide line. Because many of the intertidal nemertine species preferably hide under stones or algae (MCINTOSH, 1873; FRIEDRICH, 1935; EASON, 1973; MANE-GARZON & DEI-CAS, 1973; GIBSON, 1982) special attention was given to such epibenthic structures. In the study area the most common hard substrate is made up of blue mussels (*Mytilus edulis*) with attached bladder wrack (*Fucus vesiculosus*). After assessing the preferred habitats of the two nemertine

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**Fig. 1.** Study area ‘Nord-Sylter Wattenmeer’ in the Northern Wadden Sea. Dots indicate sampling stations on tidal flats (shaded).
species, field experiments were conducted to examine their impact on their respective prey species around their dwellings. Laboratory experiments were carried out to test whether prey behaviour is an important factor within the considered predator-prey pairs.

2. METHODS

2.1. AREA

Sampling and field experiments were carried out near the island of Sylt in the Northern Wadden Sea (Fig. 1). The study area consists of sandy and muddy tidal flats with a tidal range of 1.8 m (for details see Reise, 1985a). Mussels regularly occur throughout most of the area as detached clumps originating from mussel beds located near the low water line. Larger clumps are relatively fixed to the sediment, and are only moved during storms or by ice floes. They provide a relatively stable micro-habitat on the tidal flats, at least during summer (Thiel, 1992). Single mussel clumps cover an area from 0.01 to 1 m², but most of them are in the lower size range between 0.05 and 0.2 m².

2.2. SAMPLING

Two transects between high and low tide line were sampled in 1991 and 1992 (Fig. 1). The transect Nilssonwatt (3 stations) was sampled in July/August 1991. Water depth during mean high tide is 0.4, 0.8 and 1.6 m at the stations 'high', 'mid' and 'low', respectively. The transect Oddewatt (4 stations) was sampled in July 1991, November 1991 and March 1992. In the Oddewatt water depth during mean high tide is 0.4, 0.7, 0.9 and 1.7 m at the stations 'high', 'upper mid', 'lower mid' and 'low'. Sediment samples of 500-cm² surface area were taken with a metal box corer to a depth of about 15 cm, immediately emptied into a bucket, and then sieved in the field with a 1000-µm mesh for macrofauna.

Nemertines are able to vary their body diameter considerably. Preliminary studies revealed that specimens with <3 cm of extended body length are not retained quantitatively in the 1000-µm mesh. Therefore only nemertines ≥3 cm were counted. The same was applied to Nereis diversicolor in order to standardize the procedure, and to avoid strong interference with fast-growing juveniles during field experiments.

Two types of sediment samples were taken: either sediment containing a naturally established mussel clump or sediment without such a mussel clump. Of each type 6 samples were taken at every transect station.

In order to investigate more closely the numerical relationship between Lineus viridis and Nereis diversicolor, additional sediment samples with mussel clumps were taken and treated the same way as explained above. To determine the relation between Amphiporus lactiflores and Gammarus locusta, mussel clumps without underlying sediment were collected, sieved over a 500-µm mesh and sorted for the macrofauna. When the 500-µm sieve was used, all nemertines of at least 1 cm length were counted.

2.3. FIELD EXPERIMENTS

We altered the abundance of nemertines in the field in order to look at the prey response to high and low predator densities. The low mobility of nemertines enabled us to design the field experiments without cages. We either transferred whole mussel clumps with their initial nemertine stock or let additional nemertines crawl into the clumps, thus maintaining the natural habitat structure.

Based on the transect results, mussel clumps with many (from the high intertidal), few (mid tide line), and no Lineus viridis (low tide line) were transferred into an area of 100 x 200 m at the mid tide level in the Nilssonwatt. Of each type, 30 clumps of about 500 cm² size were placed randomly in the experimental field. Two and 4 weeks after the start of the experiment, 6 replicates of each treatment were taken and handled in the same way as the transect samples (see 2.2).

Analogously, Amphiporus lactiflores was transferred into a region with high numbers of Gammarus locusta in the mussel clumps (Möwenbergwatt, Fig. 1). Within an area of 100 x 200 m, 30 mussel clumps of about 500 cm² in size and a similar amount of algal cover were chosen for the experiment. To each of 15 of these clumps 10 A. lactiflores were added. The nemertines crawled into the cluster of mussels within 2 min. The other 15 mussel clumps served as controls. After 2 d the first 6 clumps of each type were collected. The remaining mussel clumps (6 of each type) were sampled 4 d later. One control and one experimental clump were lost during the experiment. The mussel clumps without the underlying sediment were taken and sieved for macrofauna over a 500-µm mesh.

2.4. LABORATORY EXPERIMENTS

Six experimental aquaria (400 cm² bottom area) with sediment and small mussel clumps (100 cm²) were stocked with 10 Lineus viridis each. Six aquaria without any nemertines served as controls. Five Nereis diversicolor were then added to each aquarium. The number of swimming polychaetes in each aquarium was recorded once per min for 1 h.

Analogously, 50 Gammarus locusta were added to the 6 aquaria with 10 Amphiporus lactiflores each and to each of the 6 control aquaria. At the bottom were small clumps of mussels with algae. The swimming response was measured by means of the number of amphipods which bumped into the front
window of the aquaria within 60 seconds. After all 12 aquaria had been recorded once, we started again in the same order until 18 records were taken from each. The experiment lasted 4 h.

3. RESULTS

3.1. DISTRIBUTION OF NEMERTINES

Both nemertine species prefer mussel clumps as a micro-habitat with highest abundance in the upper intertidal at both transects (Fig. 2). In the Oddewatt, *Lineus viridis* occurred in 81% of all 72 samples containing mussel clumps which were sampled between July 1991 and March 1992. Only 21% of the 72 samples without mussel clumps contained this nemertine. The maximum abundance of *L. viridis* was 41 individuals per 500 cm² with mussel clumps and 1 individual per 500 cm² without mussel clumps.

Even higher is the preference for mussel clumps by the nemertine *Amphiporus lactifloreus* (Fig. 3). In 61% of all 72 samples with mussel clumps collected in the Oddewatt this nemertine was found, whereas it only occurred in 3% of the samples without mussel clumps. The highest abundance of *A. lactifloreus* in mussel clumps was 22 individuals per 500 cm² in contrast to never more than 3 nemertines in sediment samples without mussel clumps.

For both nemertine species a seasonal trend is discernible with high numbers in summer. Until late autumn, the population declines and in early spring high abundance is back again, particularly in *L. viridis*. 
3.2. RELATIONSHIP BETWEEN NEMERTINE AND PREY ABUNDANCE

Only few Nereis diversicolor live under mussel clumps that contain high numbers of Lineus viridis (Fig. 4A). Under mussel clumps with no or only few nemertines many nereids may be present but not necessarily so. Prey numbers were inversely correlated with increasing predator numbers (Spearman-rank-correlation, p<0.05).

Similarly, Gammarus locusta was found only in small numbers in mussel clumps containing >5 Amphiporus lactifloreus (Fig. 4B). However, no significant correlation was found between numbers of A. lactifloreus and G. locusta (Spearman-rank-correlation, p>0.05).

3.3. FIELD EXPERIMENTS

Mussel clumps transplanted from high, mid and low tide levels to an experimental site at mid-tide level maintained their original high, mid and low abundances of Lineus viridis throughout the experiment (Fig. 5). In contrast, the abundance of Nereis diversicolor under mussel clumps containing many L. viridis decreased continuously and was significantly different from the other two types of mussel clumps after 4 weeks (Mann-Whitney-U-test, p<0.05). The slow decrease suggests that nereids did not try to escape under the conditions of the experiment, but were captured by the nemertines. The relatively constant number of nereids under the other two treatments proves that only high nemertine abundance caused losses in the population of N. diversicolor during the experimental period.

Experimental addition of Amphiporus lactifloreus to mussel clumps in an area with few A. lactifloreus but plenty of gammarids caused a massive escape of Gammarus locusta within 2 d (Fig. 6). While gammarid densities in control clumps were about 200, almost none were present in the experimental clumps (Mann-Whitney-U-test, p<0.05). At this time, abundance of A. lactifloreus was still significantly higher under experimental compared to control clumps (Mann-Whitney-U-test, p<0.05). Four days later, these differences in predator and prey abundances between treatment and control had disappeared (Mann-Whitney-U-test, p>0.05). Apparently, in the absence of prey, the nemertines dispersed and entered adjacent control clumps, followed by an escape response of their prey.
Amphiporus lactifloreus

Gammarus locusta

Fig. 6. Abundance of Amphiporus lactifloreus and Gammarus locusta in clumps of mussels with 10 A. lactifloreus added (treatment) and control clumps (none added) in Möwenbergwatt, October 1991. Presented are means at day 2 (n=6) and day 6 (n=8) after start of experiment. Samples were sieved with a 500-µm mesh.

3.4. LABORATORY EXPERIMENTS

In aquaria, Nereis diversicolor responded to the presence of Lineus viridis with prolonged swimming behaviour (Fig. 7). For more than 1 h the polychaetes swam continuously, only interrupted by short intervals of about 1 min, while in the control aquaria they quickly sank to the bottom and buried into the sediment. The initial decrease in polychaete numbers swimming in the aquaria with L. viridis was in part due to predation by the nemertines, thus shadowing the overall result.

The amphipod Gammarus locusta swam more hurriedly in aquaria with Amphiporus lactifloreus than in the controls (Fig. 8). When encountering a nemertine, G. locusta darts into the water column. Although during the experiment the swimming activity of G. locusta in both types of aquaria declined continuously, it prevailed on a higher level where A. lactifloreus was hidden in small clumps of mussels at the bottom of aquaria.

4. DISCUSSION

This study revealed an inverse relation of abundance between two nemertine species and their respective prey in clusters of mussels in the intertidal zone of the Wadden Sea. From experimental evidence we conclude that these distributional patterns are partly caused by the refuging behaviour of the prey organisms.

4.1. DISTRIBUTION OF NEMERTINES

The nemertines Lineus viridis and Amphiporus lactifloreus prefer the upper intertidal. This was already shown for L. viridis by NORDHAUSEN (1988) and from the rocky intertidal EASON (1973) reports the same distribution pattern for L. ruber, A. lactifloreus and five other nemertine species. Most nemertine species and higher nemertine densities are reported from the intertidal areas (MCINTOSH, 1874; COE, 1943; GIBSON, 1972; VERNET & ANADON, 1991). This pattern may be biased through the intensive research effort devoted to these areas as compared to the less accessible subtidal areas.

Benthic nemertines live either within the sediment or hide under epibenthic structures such as stones, shell gravel, mussels, algae, etc. (FRIEDRICH, 1935;...
Gibson, 1972; Eason, 1973). The strong preference for mussel clumps in the study area may be related to reproduction, as L. viridis fixes its spawn to hard substrate (Bartolomaeus, 1984) or to feeding purposes, as the preferred prey of A. lactifloreus gathers under algae during low tide. In mussel clumps, both nemertine species may also find shelter from epibenthic predators which are less efficient feeders in more complex habitats than in unstructured soft-bottom sediments (Reise, 1977; Peterson, 1979, 1982; Summerson & Peterson, 1984; Witman, 1985; Mattila, 1992).

Nemertines in the intertidal mostly feed during nocturnal low tides (Roë, 1970, 1971, 1976, 1979; Mcdermott, 1976b; Nordhausen, 1987, 1988; Rowell & Woo, 1990). They appear at the surface 10 to 30 min after the tide has receded (Roë, 1971; Thiel, 1992), while only small numbers have been observed during high tide (Roë, 1971, 1976). As a consequence, low nemertine abundance close to the low-water line may be explained by the limited time available to catch prey. In the upper intertidal, there is more time to pursue prey when it cannot escape by swimming, and more time to move about in order to find high prey densities. Low predation by important epibenthic predators in the upper intertidal zone may also be a relevant factor (Reise, 1985b). There are no reports of shorebirds feeding on nemertines.

4.2. PREY RESPONSES TO NEMERTINES

An anti-predator response may rely on visual contact (Brenchley, 1986) but often depends upon chemical substances emitted by the predators (MAYO & MACKIE, 1976; Zimmer-faust, 1989; Marko & Palmer, 1991). A frequent behavioural reaction of prey to a predator is emigration from its innate habitat (Ambrose, 1984; Olafsson & Persson, 1988; Shi, 1987; Rönn et al, 1988). As an emigrant mostly aims for a predator-free refuge (a spatial refuge—sensu Woodin 1978), this anti-predator response is best described with the term 'refuging'. This response may lead to a negative correlation between predator and prey abundance, which should not be equated with direct effects of prey capture. Indirect effects are in many cases more important as structuring mechanisms than direct effects.

Shi (1984) postulated that if prey response dominates over predator response, a negative correlation is to be expected between predator and prey spatial distribution. The inverse relation of abundance between nemertines and their respective prey in the field indicates the domination of prey response, which is further corroborated by the laboratory experiments where the prey species showed a prolonged escape response in the presence of the predator. This prey response was not evident for Nereis diversicolor and Lineus viridis in the field experiment, where the polychaetes did not react immediately to the nemertines.

A possible explanation is the sedentary mode of feeding during summer when N. diversicolor remains for long periods of time in the same burrow filtering food out of the water column (Esselink & Zwarts, 1989). However, during periods of migration to new sites, the sensitivity of N. diversicolor to the presence of L. viridis may lead to alternate abundances. When drifting in tidal currents, a prolonged swimming period of 5 or 10 min may be long enough to avoid tidal flats where large numbers of L. viridis live in the sediment or in mussel clumps scattered over these sediments.

The amphipod Gammarus locusta is much more mobile than N. diversicolor and rapidly escapes from the nemertines in the field. This escape behaviour seems to be effective when low numbers of Amphiporus lactifloreus are present. In areas where almost every mussel clump houses several A. lactifloreus, no safe refuges are available for G. locusta. On such tidal flats G. locusta was only found in very low abundances (Thiel, 1992).

Regarding the different life-styles and tendency to perform the refuging behaviour, the following distinction can be hypothesized between the two investigated prey species: experimental data suggest that N. diversicolor may show refuging behaviour during periods of migration, thus avoiding its nemertine predator in advance (avoidance behaviour). G. locusta reacts to its predator every time an encounter happens, thus trying to escape the menace of an attack (escape behaviour).

Both prey species perform their refuging behaviour only during high tide. During low tide, when these swimming responses are inhibited, the prey is vulnerable to nemertine attacks (Roë, 1970, 1971, 1976, 1979). McDermott (1976b) reported that Cerebratulus lacteus feeds successfully on the bivalve Ensis directus during low tide but might be less effective during high tide, because then the bivalves may leave their burrows and swim away.

4.3. EFFECTS OF ENDOBENTHIC PREDATORS

It has been stated that in the intertidal zone predators may at times control prey populations (Reise, 1985b). In particular, high prey abundances inside cages excluding epibenthic predators has led to this conclusion. The wide occurrence, reported feeding rates, and enclosure experiments suggested that endobenthic predators are also likely to diminish prey populations considerably (Committo & Ambrose, 1985a, 1985b). However, we propose here that the effects of endobenthic predators on their prey populations are different from those of epibenthic predators. As an encounter with epibenthic predators such as birds, fish and crabs in tidal flats is almost unpredictable due to their high mobility, the only chance for benthic prey is a direct escape response such as retreating down into burrows or withdrawing soft body parts into a shell. In this case, a decrease in prey number...
results from prey consumption. In the other case, when both predator (disturber) and prey dwell in the sediment, a promising option for the prey to avoid encounters is emigration (AMBROSE, 1984d). With the help of tidal currents a considerable distance between predator and prey may be achieved within a short time. This may result in conspicuous effects on the distribution of prey in time and space, which can, by far, exceed the effects of direct prey capture. Experimental designs in the laboratory and in the field which did not allow the prey to perform its escape behaviour, may have prompted investigators to overestimate the predators' capture and consumption rates. On the other hand, the refuging behaviour of benthic prey in response to endobenthic predators gives rise to a disproportional effect on prey distribution, and thus this interaction has strong ecological implications.

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