



Preying at the edge of the sea: the nemertine *Tetrastemma melanocephalum* and its amphipod prey on high intertidal sandflats

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Abstract

In the European Wadden Sea, the nemertine *Tetrastemma melanocephalum* occurs together with its prey, the amphipod *Corophium arenarium*, in the upper intertidal zone. *T. melanocephalum* leaves the sediment when the tide has receded and captures *C. arenarium* in its U-shaped burrow. Highest abundances of *T. melanocephalum* on the sediment surface were found on summer evenings, 2–4 h after high tide, when just a thin film of water was left on the flats. Laboratory Y-maze experiments indicated that gradients of substances produced by *C. arenarium* in this film of water play a role in tracking the prey. In the field, *T. melanocephalum* appeared in significantly higher numbers on experimental high density patches of *C. arenarium*. The amphipod in turn is able to recognize the nemertine. In aquarium experiments, significantly more amphipods escaped from the sediment into the water column when the predator was present. In the field, both predator and prey showed a high mobility by drifting in tidal waters. Benthic abundance maxima of *T. melanocephalum* and *C. arenarium* usually did not coincide spatially. It is assumed that the nemertines avoid tidal flats that dry out quickly leaving too little time for prey capture. *T. melanocephalum* is not able to dig into the sediment, but lives in burrows of *Nereis diversicolor*. The abundance of this polychaete was inversely related to *C. arenarium*, presenting a dilemma for *T. melanocephalum*: the spatial overlap of food and accommodation was rather small.

Introduction

The amphipods *Corophium arenarium* (Pallas) and *Corophium volutator* Crawford are dominant species in upper zones of many intertidal flats of the North Atlantic Ocean (Hart, 1930; Muus, 1967; Bousfield, 1973; Larsen & Doggett, 1991). They appear in high abundances, *C. volutator* up to 118 000 ind. * m⁻² (Andres, 1970), and are important food for migratory shorebirds (Bengtsson & Svensson, 1968; Goss-Custard, 1977; Boates & Smith, 1979; Hicklin & Smith, 1981; Peer et al., 1986; Raffaelli & Milne, 1987; Wilson, 1989, 1990), fishes (Smidt, 1951; Imrie & Daborn, 1981; Dadswell et al., 1984; Mattila & Bonsdorff, 1989), crabs (Hart, 1930; Linke, 1939), shrimps (Plagmann, 1939) and polychaetes (Muus, 1967; Commito, 1982; Ambrose, 1984a; Commito & Schrader, 1985).

Distributional segregation of both species seems to be mainly determined by sediment composition: *C. volutator* lives in muddy, *C. arenarium* in more sandy sediments (Watkin, 1941; Meadows, 1964; Flach, 1993, 1996). Populations of *Corophium* spp. have long been known to exhibit largely unexplained spatial and temporal fluctuations in density (Watkin, 1941; Muus, 1967; Reise, 1978; Ólafsson & Persson, 1986; Wilson, 1988; Beukema & Flach, 1995, Wilson & Parker, 1996). Some studies highlight the significance of parasites (Jensen & Mouritsen, 1992; Jensen et al., 1998), others explain intertidal zonation patterns with interactions of *Corophium* spp. with associated species. According to Beukema & Flach (1995), the upper *Corophium* limit is set by abiotic factors and the lower limit by biotic interrelations. On their transects, the lower *Corophium* limit coincided with the upper level

of high densities of adult lugworms *Arenicola marina*. Sediment reworking by this polychaete is likely to have a strong negative impact on *Corophium* spp. (Cadée, 1976; Jensen & Kristensen, 1990; Flach & de Bruin, 1992, 1994; Flach, 1993; Beukema & Flach, 1995). Similar disturbance effects are caused by dense aggregations of cockles *Cerastoderma edule* (Jensen, 1985; Flach, 1992, 1993; Flach & de Bruin, 1994) and by the polychaete *Nereis diversicolor* (Rönn et al., 1988; Jensen & André, 1993). Both species increased migration rates of *Corophium* spp. in laboratory experiments. Earlier findings of *N. diversicolor*, being also an important predator of *Corophium* spp. (Muus, 1967; Goerke, 1971; Rönn et al., 1988), could not be corroborated (Jensen & André, 1993). Instead, it was found that *N. diversicolor* is mainly a suspension and deposit feeder (Reise, 1979; Esselink & Zwarts, 1989; Riisgaard, 1991).

In contrast, the nemertine *Tetrastemma melanocephalum* (Johnston) is an obligatory predator, which does feed on *Corophium volutator* (Bartsch, 1973, 1975, 1977). *T. melanocephalum* attacks the amphipod with its long proboscis, which is everted within fractions of a second. A stylet at the end of the proboscis pierces the exoskeleton of the amphipod and toxins and enzymes are injected – the toxins immobilize *C. volutator* within seconds and the enzymes predigest prey tissue (Gibson, 1972). The nemertine then sucks out the amphipod (Bartsch, 1973, 1975). Prey capture normally happens inside the U-shaped burrow of *C. volutator*. *T. melanocephalum* enters the burrows from the sediment surface when the tide has receded and a thin film of water is left on the flats (Bartsch, 1973, 1975). Although infaunal predators are known as an important structuring force in benthic communities (Commuto & Ambrose, 1985a; Ambrose, 1991), the role of *T. melanocephalum* in the *Corophium*-community has not yet been elucidated. Reports on distribution of *T. melanocephalum* on intertidal flats suggest that *Corophium* spp. are specific prey for *T. melanocephalum* because an association with either *Corophium volutator* (Bartsch, 1973, 1975, 1977; Reise, 1978, 1985) or *C. arenarium* (Gibson, 1995) is always mentioned. However, abundance of *T. melanocephalum* has rarely been quantified, and the intertidal zonation has not been determined yet. Likewise, the complex interactions between this nemertine and its prey exceeding pure predation have not been studied. Predatory interactions are subject to a considerable number of variables (Murdoch & Oaten, 1975) relat-

ing to characteristics of predator, prey and their special environment.

Nemertines are often neglected in interactions between species (McDermott, 1984, 1993), although their predatory effects can lead to a substantial decrease in prey density (Ambrose, 1991). The nemertines *Amphiporus lactifloreus* and *Lineus viridis* may force escape behaviour of their prey (Thiel, 1992; Thiel & Reise, 1993). Predator avoidance behaviour in the marine benthos is also mentioned by many authors (Witte & De Wilde, 1979; Commuto, 1982; Peterson et al., 1982; Ambrose, 1984b; Commuto & Ambrose, 1985a,b; Ólafsson & Persson, 1986; Rönn et al., 1988). It may have strong effects on prey distribution while the actual consumption of prey may be relatively modest (Thiel & Reise, 1993). If the predators depend on special features of the habitat, predatory effects can be concentrated in special zones or structures. For instance, *A. lactifloreus* and *L. viridis* occur preferentially in clusters of blue mussels (*Mytilus edulis*). Both predators and their respective prey show inverse relationships in these clusters along the tidal slope, which is explained by refuge behaviour of the prey (Thiel & Reise, 1993). For *T. melanocephalum*, a dependence on the burrows of *N. diversicolor* has been described (Bartsch, 1977).

The purpose of this study was to examine whether *T. melanocephalum* contributes to the zonation pattern in an upper intertidal sandflat inhabited by *C. arenarium* and *N. diversicolor*. On the one hand, we investigated whether abundance maxima of *T. melanocephalum* and *C. arenarium* coincided. Furthermore, direct interactions between predator and prey were elucidated: laboratory experiments were carried out to test whether *T. melanocephalum* tracks its prey by perceiving cues in the water produced by *C. arenarium* and whether *C. arenarium* in turn reacts to the presence of *T. melanocephalum* by escape. In a field experiment, we examined if *T. melanocephalum* invades experimental high density patches of *C. arenarium*.

Materials and methods

Description of sites studied

Sampling and field experiments were carried out on the tidal flats near the peninsula of Eiderstedt in the Northern Wadden Sea (Figure 1). The flats lie sheltered between the mainland and a sandbank, which

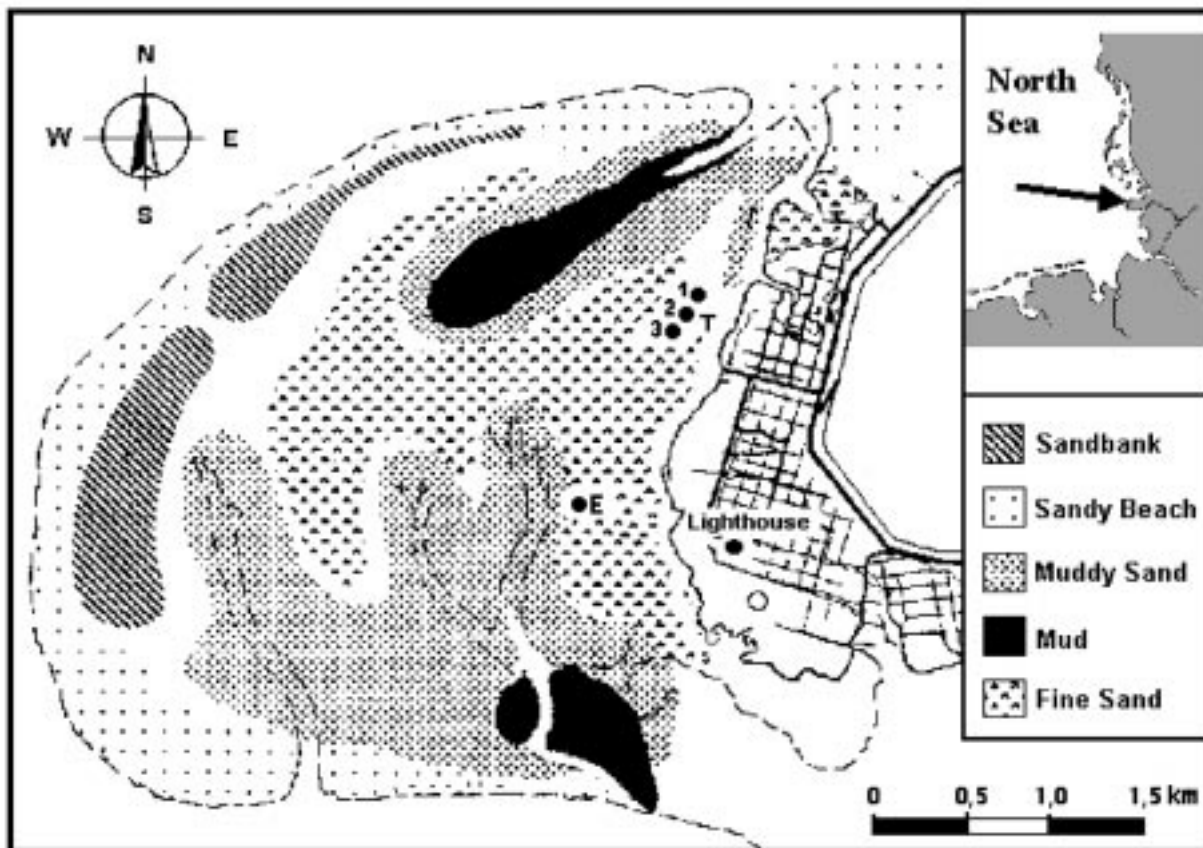


Figure 1. Study area with sediment zonation pattern of the flats. 'E' experimental site; 'T' transect through the upper intertidal with three sites, site 1 as the lowest.

is not submerged during regular high tides. Tidal range is about 3 m. Southwesterly winds prevail and blow fine grained sand from the sandbank onto the flats. Mean grain size of the sediment is 0.125–0.25 mm (Brey, 1991).

Tidal heights of sampling and experimental sites were estimated over several high waters using field observations. These observations for each site were later calibrated using the measured high water levels and tidal curves obtained by the gauge 'Kolumbusloch' near the Westerhever Sandbank.

Sampling

Abundances of *Tetrastemma melanocephalum* were estimated via surface activity, abundances of *Corophium arenarium* and *Nereis diversicolor* via sediment samples and abundances of *Arenicola marina* via counting the lugworm castings on 100 m² plots. These different methods were used because abundances of *T. melanocephalum* and *A. marina* were too low to be de-

termined by sediment samples. All investigations were carried out along a transect with three sites through the upper intertidal (Figure 1). In addition, the surface activity of *T. melanocephalum* in the lower intertidal was determined occasionally (on 10 days, between 10 July and 25 August 1994, at two sites below the transect).

T. melanocephalum was quantified during periods favourable for surface activity (i.e. in the evening, 7:00–10:30 pm, on exposed flats with a water film). Nemertines crawling on the sediment surface of plots of 100 m² (in a few cases 25 and 50 m²) were counted from mid June until the end of August in 1994. To avoid disturbing the same plot by footprints, counts alternated between four plots of 100 m² placed side by side at each transect site.

Sediment samples of 110 cm² surface area were taken with a plastic tube corer to a depth of 15 cm and sieved through a 500 μm mesh in the laboratory.

Field experiment

In 1995, we added *C. arenarium* to experimental plots in order to investigate whether *T. melanocephalum* would invade them. This experiment was conducted in the transition zone between *C. arenarium* and *Arenicola marina* beds (Figure 1 ('E')) with naturally low densities of *C. arenarium*. On one evening in July, at low water, we placed about 20 000 *C. arenarium* on each of six circular plots of 0.5 m². Six plots served as controls without prey addition. Plastic rims kept *C. arenarium* on the plots and were removed when *C. arenarium* had settled after 1 h. All plots were placed in an area of 8 * 10 m, each in the middle of 1 m² areas where *Arenicola marina* was naturally absent. According to the given pattern of *A. marina*, the plots were arranged irregularly with a distance of at least 1 m between them. Four days after prey addition, we counted the nemertines on the flats during their activity period.

Laboratory experiments

Aquarium experiment

To test whether *C. arenarium* escapes from *T. melanocephalum*, 12 experimental aquaria (20 * 20 * 20 cm) were stocked with sediment (8 cm depth; passed through a 300 µm sieve, from *C. arenarium*-habitat) and about 300 *C. arenarium* each. The sediment was covered with a thin film of water, simulating low-tide conditions. After 1 day when *C. arenarium* had settled, *T. melanocephalum* were inserted into six aquaria as predator addition. The other six aquaria served as controls without predators. All replicates were kept along a row of windows and exposed to a natural day/night-rhythm with the two treatments in alternate order. Then, during daytime, all replicates were flooded with 2 dm³ of seawater, one after the other. To avoid disturbance of the sediment surface, a plastic foil was placed on the sediment surface before flooding and removed immediately afterwards. Directly after this in the same order, all swimming *C. arenarium* were removed with a pipette, which took about ten minutes for each replicate. All replicates contained standing seawater and had no outflow through which the amphipods could escape. Those *C. arenarium* remaining in the sediment were sieved out and both were counted. For each replicate, the percentage of swimming *C. arenarium* was calculated from the sum of swimming *C. arenarium* and those remaining in the sediment. The whole experiment was repeated four times. In

the first three experiments, 10 nemertines were added into each predator-replicate and the amphipods were exposed to predatory impact for 1–2 days. In the 4th experiment, only one nemertine was inserted and the amphipods were exposed to predatory impact for 5 days. In the four experiments, *C. arenarium* and *T. melanocephalum* were re-used, only the dead ones were replaced. The animals were set back into the same aquarium where they had been before. This was done because we did not know how long *C. arenarium* would need to adapt to laboratory conditions.

Y-maze experiment

A Y-maze experiment was performed to test if *T. melanocephalum* is able to perceive *C. arenarium* through the water. From a 100 dm³ tank, seawater ran trough tubes (ϕ 12 mm) into two dishes (13 * 21 cm), which were arranged parallel, each dish in longitudinal direction. One dish contained about 2000 *C. arenarium*, the other none. Out of each dish, the water ran through a tube of 20 mm ϕ into a single dish (9 * 21 cm), filled with 4 mm of sediment and containing one *T. melanocephalum*. The water left the Y-maze out of this dish through 20 mm-tubes. A 200 µm gauze was installed to keep the animals within the dishes, except for the tubes leading water into the nemertine dish. *T. melanocephalum* was placed in the middle of the nemertine-dish and could now decide to move into one of these tubes. When it had crawled through one, it was removed and another nemertine was inserted. Prior to the experiment, we tested if a non-turbulent flow would establish a gradient in the nemertine dish that *T. melanocephalum* could orientate on during crawling back and forth by putting ink into one *C. arenarium* dish. In the first run, the reaction of 28 nemertines was tested, in a second run for artefact control *C. arenarium* was put into the other dish and 20 of the same nemertines had to make their choice again. A final test with no *C. arenarium* in either dish was conducted with 9 nemertines. Before each run, the 100 dm³ tank was filled with 200 µm- filtered seawater and between runs the experimental apparatus was rinsed with new seawater. The outflow rate was adjusted to about 1 dm³ min⁻¹ and the water level in the dishes was kept between 2 and 2.5 cm. The whole experiment was conducted in a dark room under red light.

Observations on the behaviour of the nemertines and amphipods

In the field, we investigated the behaviour of *T. melanocephalum* and *C. arenarium* drifting in tidal waters. In the laboratory, we offered alternative prey (two amphipods, one isopod and one harpacticoid copepod) to *T. melanocephalum* and observed prey capture behaviour.

Results

Surface activity of *T. melanocephalum*

T. melanocephalum was active on the sediment surface in summer, we could not find it there in winter. In 1994, only single individuals were present in May, activity increased in June and reached a maximum in July (8 ind. m⁻²; Figure 2). In August and September, densities decreased again.

T. melanocephalum left the sediment when the tide had receded and reached highest surface activity on summer evenings, between 2 and 4 h after high tide. For best estimates of abundance, surface activity of *T. melanocephalum* was determined during these periods. During high tide and at night, only very few individuals were found.

Spatial distribution of the predators and the prey

Looking at the whole tidal slope, *T. melanocephalum* preferred the upper intertidal like its prey *C. arenarium* (Beukema & Flach, 1995). In the lower intertidal, surface abundances of *T. melanocephalum* were on average 5% of overall abundance, which was counted in the whole intertidal.

Within the upper intertidal, *C. arenarium* was most abundant at the uppermost site of the transect, while *T. melanocephalum* showed highest surface activity at the intermediate site (see Figure 3). *Nereis diversicolor* was also abundant at the intermediate site and reached highest densities at the lowest site. *Arenicola marina* was only found at the lowest transect site with 1–2 ind. m⁻² (Table 1).

Mobility of the predators and the prey

T. melanocephalum and *C. arenarium* both drifted in the water column. *C. arenarium* actively held its position in the water. *T. melanocephalum* adopted a long, slender shape – nearly twice as long compared

Table 1. Tidal height and submersion of sampling (transect: 1, low – 3, upper) and experimental (E exp.) sites and abundances *A. marina*; submersion data of the transect for June–August 1994, for the experiment June–August 1995. (MHW: 138 cm above MTL)

| Site | Tidal height below MHW [cm] | Mean submersion time / tide [h:min] | % of non-flooding tides | <i>A. marina</i> [ind m ⁻²] |
|---------|-----------------------------|-------------------------------------|-------------------------|---|
| 1 low | 34 | 2:53 | 4 | 2 |
| 2 mid | 16 | 1:57 | 17 | 0.02 |
| 3 upper | 8 | 1:33 | 34 | 0 |
| E exp. | 27 | | 12 | 1–2 |

to when it is crawling. Drifting *T. melanocephalum* were mainly found during flood and in water depths between 5 and 30 cm. By walking through the water, we counted up to one nemertine m⁻¹. Several times we observed that *T. melanocephalum* coiled up and sank to the sediment. By producing mucus, they tried to attach to the sediment, presumably in order to search for a burrow to vanish in. Observations in aquaria indicate that *T. melanocephalum* can only hold its position in the water in the presence of currents. In the field, *T. melanocephalum* sank to the ground when they were isolated from the currents by lowering perspex cylinders around them.

Direct interactions between *T. melanocephalum* and its prey

In order to test whether *T. melanocephalum* would accept prey organisms other than *C. arenarium*, four crustacean species were offered in plastic jars (ϕ 8.7 cm) with different water levels. Several individuals of *Talorchestia brito*, a semi-terrestrial amphipod (7–14 mm in length), were attacked and sucked out in jars with few water, when they were unable to swim. In jars filled with 1 cm of water, *T. melanocephalum* did not capture them. The same was found for *Bathyporeia* spp., a very mobile species in the field. *C. arenarium*, on the other hand, could be captured in jars with 1 cm of water. One 10 mm long *Idotea balthica* was killed and sucked out by a 10 mm long *T. melanocephalum*.

For juvenile *T. melanocephalum*, harpacticoids may play an important role. In the laboratory, one 4 mm long and 0.3 mm broad *T. melanocephalum*, which had starved for one month, fed on 5 *Mesochra lilljeborgi* (0.3–0.5 mm) and afterwards one juvenile *C. arenarium* (1.5 mm in length).

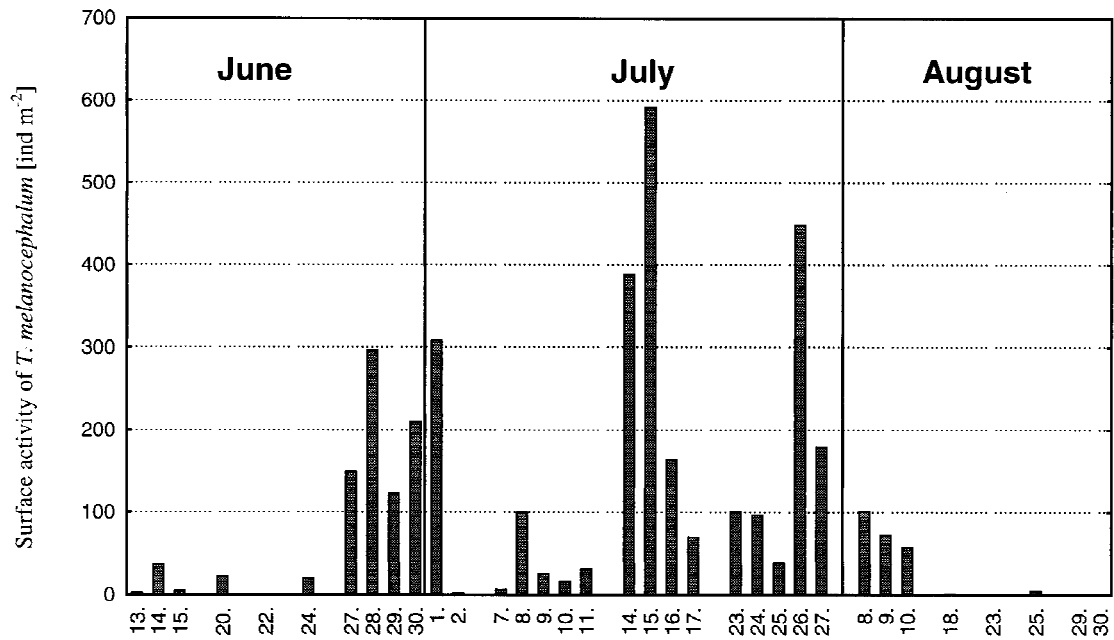


Figure 2. Surface activity of *T. melanocephalum* in summer 1994, mean values of the lowest and intermediate sites on a transect within the upper intertidal for single days, except for: 13–24 June lowest site only; 24 July, 18, 29–30 August intermediate site only. Sites were only counted at the given dates, spaces between the dates on the x-axis indicate an interruption of counting for one or more days.

Perception of prey by *T. melanocephalum*

In the laboratory Y-maze experiment, *T. melanocephalum* preferred the tube originating from the *C. arenarium* dish over the other tube carrying neutral seawater. In the first run, 26 individuals of *T. melanocephalum* decided for the '*C. arenarium*-tube' and two for the other. In the cross check, when *C. arenarium* was put into the other dish, we found the same preference of the '*C. arenarium*-tube'. In the blank check, when there was no *C. arenarium* in either dish, *T. melanocephalum* was undecided. The nemertine took twice as long to decide for one tube compared to when *C. arenarium* was in one of the dishes. In the first two runs, we observed several *T. melanocephalum* attacking the tweezers when we removed *T. melanocephalum* from the experiment after it had crawled through the *C. arenarium*-tube.

Tracking of prey by *T. melanocephalum*

In the field, *T. melanocephalum* reacted to experimentally increased density of *C. arenarium*. Four days after prey addition, significantly more *T. melanocephalum* were counted on the *C. arenarium* plots (29 ± 21 ind. 0.5 m^{-2} ; mean \pm SD) compared to controls (3 ± 2 ; Mann-Whitney-*U*-test, $p < 0.05$). Prior to the experi-

ment, a natural density of 15 ± 37 *C. arenarium* m^{-2} was determined. Abundance of *Arenicola marina* was 1–2 ind. m^{-2} and of *Nereis diversicolor* 503 ± 230 (ind. m^{-2} ; mean \pm SD).

Escape from the predator by *C. arenarium*

C. arenarium was able to detect *T. melanocephalum* and escaped into the water column when the predators appeared in high abundances. However, this result was obtained only in the 2nd and 3rd aquarium experiment. The three experiments were carried out one after the other, re-using the animals. In the first experiment, swimming activity of *C. arenarium* did not depend on the presence of *T. melanocephalum*, but in the following two experiments it did (Table 2). In the first experiment, *C. arenarium* showed a very high swimming activity (mean 63%) in both treatments, in the following two experiments a much lower one (2nd experiment: mean 28%, 3rd experiment: mean 24% in the presence of the predator and 6% resp. 3% in the absence of predators, Mann-Whitney-*U*-test, $p < 0.05$). In a 4th experiment with only one instead of 10 *T. melanocephalum*, there was no difference in *C. arenarium* swimming activity (Mann-Whitney-*U*-test, $p > 0.05$).

Table 2. Mean percentage of swimming *C. arenarium* in aquaria with and without *T. melanocephalum*; six replicates for each treatment; *U*-test: n.s.: not significant, *: $p < 0.05$

| Experiment | Date of flooding | Number of nemertines per predator replicate | Percentage of swimming <i>C. arenarium</i> | | <i>U</i> -test | Days of predatory impact |
|------------|------------------|---|--|-----------------|----------------|--------------------------|
| | | | without nemertines | with nemertines | | |
| 1 | 24 Aug. | 10 | 63 ± 16 | 63 ± 14 | n.s. | 2 |
| 2 | 10 Sept. | 10 | 6 ± 5 | 28 ± 6 | * | 1 |
| 3 | 23 Sept. | 10 | 3 ± 3 | 24 ± 7 | * | 2 |
| 4 | 1 Oct. | 1 | 8 ± 2 | 10 ± 2 | n.s. | 5 |

Table 3. Absolute numbers of swimming *C. arenarium* and those remaining in the sediment after flooding of aquaria with and without predators (see Table 2); Σ : number of surviving amphipods per replicate

| Aquarium experiment | | | | | | | | |
|---------------------------|--------------------|----------|--------------------|--------------------|----------|--------------------|--------------------|----------|
| 1 | | | 2 | | | 3 | | |
| Amphipods swimming | Amphipods sediment | Σ | Amphipods swimming | Amphipods sediment | Σ | Amphipods swimming | Amphipods sediment | Σ |
| With 10 nemertines | | | | | | | | |
| 189 | 89 | 278 | 51 | 195 | 246 | 30 | 224 | 258 |
| 148 | 82 | 230 | 58 | 209 | 267 | 68 | 250 | 272 |
| 125 | 85 | 210 | 111 | 213 | 324 | 89 | 248 | 274 |
| 95 | 140 | 235 | 119 | 230 | 349 | 60 | 234 | 265 |
| 144 | 90 | 234 | 88 | 249 | 337 | 70 | 225 | 248 |
| 180 | 33 | 213 | 80 | 195 | 275 | 70 | 218 | 249 |
| Without nemertines | | | | | | | | |
| 123 | 84 | 207 | 5 | 249 | 254 | 2 | 260 | 281 |
| 136 | 74 | 210 | 12 | 246 | 258 | 6 | 251 | 269 |
| 136 | 160 | 296 | 15 | 267 | 282 | 5 | 252 | 281 |
| 129 | 154 | 283 | 6 | 273 | 279 | 5 | 263 | 275 |
| 185 | 94 | 218 | 23 | 268 | 218 | 25 | 240 | 218 |
| 133 | 39 | 172 | 42 | 262 | 304 | 4 | 236 | 257 |

At the end of the 2nd and 3rd experiment, methodological problems occurred because we found more than 300 *C. arenarium* in some replicates although we inserted only 300 (Table 3). Maybe we introduced small *C. arenarium* with the sediment, which grew to sizes remaining in the sieve during the experiments – *C. arenarium* was in the experimental aquaria for 5 days in the 2nd experiment and for four days in the 3rd experiment. Because of the different *C. arenarium* numbers between replicates, we calculated percentages of swimming *C. arenarium* from the sum of all *C. arenarium* retrieved from each aquarium. Numbers of *C. arenarium* were not different between treatments (Mann-Whitney-*U*-test, $p < 0.05$).

Apart from swimming, *C. arenarium* showed additional reactions to the presence of *T. melanocephalum*. In aquaria with *T. melanocephalum*, 2 days after addition of the nemertines and before flooding, fewer burrow openings of *C. arenarium* were found compared to those aquaria where the predator was absent. Burrow openings were closed with small rolls of cemented sediment. In absence of *T. melanocephalum*, *C. arenarium* accumulated mounds of sediment around the openings, giving the sediment surface quite a different appearance.

After we had flooded the aquaria and had kept them undisturbed for 2 days without aeration, another difference developed between the treatments. *C. aren-*

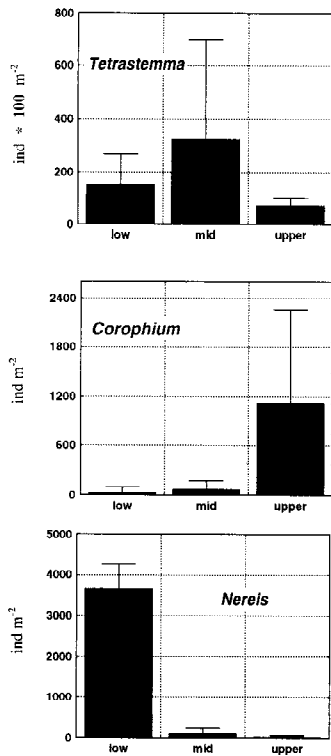


Figure 3. Surface activity of *Tetrastemma melanocephalum* * 100 m⁻² (counts on 8 days, 14–26 July 1994) and abundance of *Corophium arenarium* and *Nereis diversicolor* [ind m⁻²] (+SD) in the sediment along the transect (sampling dates of sites: upper site: 22 July 1994, intermediate (mid) site: 25 July 1994, lowest site: 27 July 1994).

arium built small chimneys around its burrows when *T. melanocephalum* was absent (Figure 4). In presence of the predator fewer and much shorter chimneys occurred.

Discussion

This study revealed that *Tetrastemma melanocephalum* is highly adapted to preying on *C. arenarium* which represents the only important prey for adult *T. melanocephalum* on high intertidal sandflats in the Wadden Sea. Other possible prey organisms were not abundant there or too mobile for being captured. However, amphipod prey that is probably poorly available for *T. melanocephalum* in nature was accepted in the laboratory. This indicates that *T. melanocephalum* is not dependent on a single prey item as was also described for other nemertines (McDermott, 1984).

Juvenile *T. melanocephalum* fed on harpacticoids in the laboratory (Bartsch, 1973; this study). This

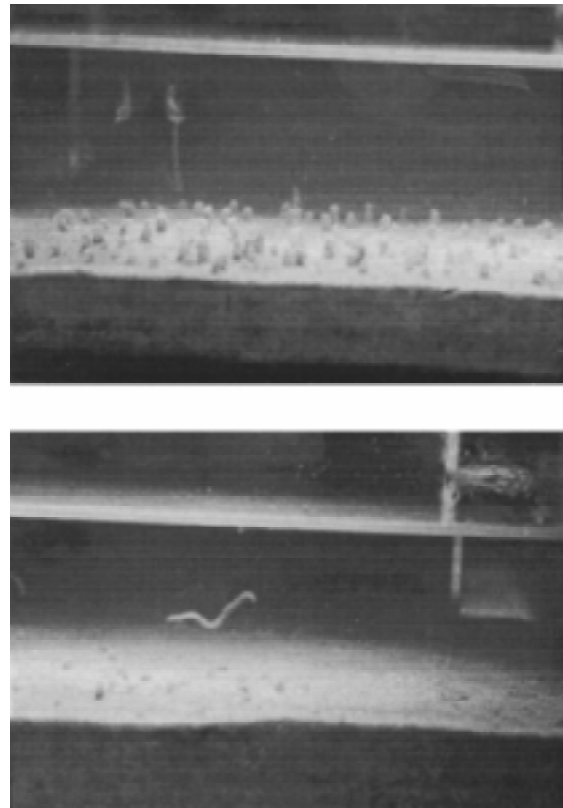


Figure 4. *Corophium arenarium*, change in the tube construction in the presence of *Tetrastemma melanocephalum*. Above: aquarium with *C. arenarium* only; below: aquarium with *C. arenarium* and *T. melanocephalum*, three days after insertion of the nemertines and two days after flooding of the aquaria. Above: shadows of swimming *C. arenarium* in the water column; below: *T. melanocephalum* on the aquarium wall; 0.5:2 cm.

may be of crucial importance for small *T. melanocephalum* until they are able to capture *C. arenarium*. Harpacticoids should be available to *T. melanocephalum* because they are highly abundant both on the sediment surface and in burrows of *N. diversicolor* (Reise, 1985), where *T. melanocephalum* receives accommodation and may raise its brood. In addition, high abundances of harpacticoids in summer may coincide with the reproductive period of *T. melanocephalum*. We observed *T. melanocephalum* spawning in July/August (Kruse, 1996).

High surface activity of *T. melanocephalum* during its spawning season may be related to mate searching, but only in part. In July/August mature *T. melanocephalum* fed 2–3 *C. arenarium* d⁻¹ in the lab (Kruse, 1996) and in the field, many immature *T. melanocephalum* were observed active on the sediment surface during this time.

Prey capture and foraging behaviour of T. melanocephalum

T. melanocephalum searches for prey during low tide, as was described for most other intertidal nemertines (Roe, 1971; Gibson, 1972; Nordhausen, 1988; Thiel & Reise, 1993; Thiel et al., 1995; Thiel, 1998). Since *T. melanocephalum* is a very small and light-weighted nemertine, low-tide activity may reduce the risk of being drifted into unfavourable sites by tidal currents. Furthermore, it has been suggested that prey cannot escape into the water column at low tide (Roe, 1970, 1976; McDermott, 1976; Thiel & Reise, 1993; Thiel et al., 1995). In the laboratory, *C. arenarium* left the sediment stocked with *T. melanocephalum* and swam into the water column when the aquaria were flooded one, resp. 2 days after the introduction of the nemertines. But *C. arenarium* can also escape the nemertines at low tide. *T. melanocephalum* captures *C. arenarium* inside its burrow. If an attacked *C. arenarium* succeeds to leave its U-shaped burrow at low tide, it can crawl faster over the sediment surface than *T. melanocephalum*. So we assume that the amphipods can equally well escape their predator at high or low tide. Escape from predator during low tide has also been found for the polychaete *Scolelepis squamata* who escapes from the polychaete *Eteone longa* (Behrends & Michaelis, 1977). Furthermore, some nemertine species successfully prey on tube-living amphipods in the subtidal, where escape into the water column is always possible (McDermott, 1976, 1988, 1993; McDermott & Roe, 1985).

Another explanation for *T. melanocephalum*'s foraging activity during low tide may be that locating of its prey by chemoreception is facilitated. During high tide, chemical substances that could lead the predator to the prey may be diluted (Atema, 1988). Chemoreception is the main means of prey detection for nemertines (Amerongen & Chia, 1982). Our experiments suggest that *T. melanocephalum*, as well, uses cues in the water to find *C. arenarium*. The rather sedentary life-style of *C. arenarium* and its pumping activity inside the U-shaped burrow may favour the development of a gradient of chemical substances around the burrow openings in the thin film of water on the sediment surface during low tide. Searching behaviour of *T. melanocephalum* observed in the field supports the assumption that it orientates on such gradients. We saw the nemertine continuously bending its head to the side while creeping over the sediment surface. Once *T. melanocephalum* had picked up a strong scent of

C. arenarium, a tactile stimulus of a moving object caused *T. melanocephalum* to eject its proboscis. In the laboratory, *T. melanocephalum* attacked tweezers after being exposed to water containing *C. arenarium*.

On a larger spatial scale, prey location may be facilitated by the flow regime. Thiel (1998) considers the steady unidirectional flow of water during low tide to offer the most favourable condition for locating prey. For scavenging nemertines, prey location was described for distances of 5–10 m (Thiel, 1998) or even up to 20 m (McDermott & Roe, 1985). However, long-distance chemoreception may be more important for scavenging nemertines than for those preying on live prey like *T. melanocephalum* (Roe, 1970; McDermott & Roe, 1985). Nemertines which prey on tube-dwelling amphipods do not have to crawl long distances since their prey often occurs in patches of relatively high densities (McDermott & Roe, 1985).

Concerning the diurnal activity rhythm, *T. melanocephalum* differs from many other nemertines. *T. melanocephalum* preferred the evening while many other nemertines are more active at night (Gibson, 1972; Thiel & Reise, 1993; Thiel et al., 1995). An adaption to higher temperatures may be one reason for the higher activity of *T. melanocephalum* during the evening compared to the night. The coincidence of the seasonal maximum of activity of *T. melanocephalum* and maximum temperatures in July may indicate such an optimum. For the nemertines *Amphiporus lactifloreus* and *Lineus viridis*, both common in the Wadden Sea, seasonal and diurnal maxima of activity also lie within the same temperature range, but at lower temperatures. These species were more active on the surface in late autumn and winter and at night (Thiel et al., 1995).

Impact of T. melanocephalum on C. arenarium

A predator may influence its prey population in different ways: by predation itself, by causing escape and avoidance behaviour and by altering of other behaviour, e.g. feeding activity. Most studies on predator-prey interactions concentrate on predation only and neglect other predatory impacts. *T. melanocephalum* may prey on 3 *C. arenarium* nemertine⁻¹ d⁻¹ (Bartsch, 1973; Kruse, 1996). In our laboratory experiments, *T. melanocephalum* increased the escape of *C. arenarium* into the water column 4–8-fold. This indicates that disturbance of the prey may also be an important factor determining prey distribution. However, results of our aquarium experiment are not quite

clear. In the first experiment, the very high swimming activity of *C. arenarium* in the treatment with and without predator posed questions. Maybe the amphipods were not yet adapted to laboratory conditions, lunar migration rhythms or mate searching activities of the amphipods could have also blurred the picture. Furthermore, the four experiments conducted in sequence were not independent from each other since the animals were re-used. Consequently, the higher swimming activity of amphipods in replicates with than without predators in those without in the 2nd and 3rd experiment may be a consequence of the exposure to nemertines in the first experiment.

Our aquarium experiment also indicated behavioural change of the prey in the presence of *T. melanocephalum*. *C. arenarium* retreated into its burrow and closed the burrow openings with sediment. This may protect *C. arenarium* from being captured because *T. melanocephalum* is not able to dig into the sediment (pers. obs.; Bartsch, 1973) and may not be able to locate *C. arenarium* in a sealed burrow. *C. arenarium* in turn probably stops feeding in closed burrows. Consequences of behavioural changes and predator avoidance should be considered in future assessments of predatory impacts.

Mobility of predator and prey

Both *T. melanocephalum* and *C. arenarium* exhibited high mobility by drifting in tidal waters. For *Corophium volutator*, drift is well described (Ólafsson & Persson, 1986; Hughes, 1988; Essink et al., 1989; Hughes & Horsfall, 1990; Lawrie & Raffaelli, 1998a,b) and is reflected by shifts in upper distribution limits due to varying tide levels (Beukema & Flach, 1995). Escape from a predator may be one reason for *Corophium* spp. to enter the water column. For *Corophium arenarium*, escape from sediment disturbance by *Arenicola marina* and *Cerastoderma edule* into the water column has been shown by Flach (1993) and from *N. diversicolor* by Jensen & André (1993). Our results reveal that *T. melanocephalum* may be an additional factor to provoke emergence of *C. arenarium*.

For *T. melanocephalum*, drift in tidal waters had not been described before and scarcely for other nemertine species with an endobenthic life style (Bürger, 1897–1907; Dean, 1978). One reason for the drift of *T. melanocephalum* may be mate searching. Drift, reproduction and high surface activity of *T. melanocephalum* all coincide in July/August. In other nemertine

species, mobility increases during reproduction as well. In Maine, specimens of *Cerebratulus lacteus* were found in driftnets in March (Dean, 1978) when this nemertine spawns (Bürger, 1897–1907). *Amphiporus lactifloreus* and *Lineus viridis* show higher surface activity on tidal flats during their reproductive periods (Thiel et al., 1995; Thiel & Darnedde, 1996).

Probably mate searching is not the only reason for drifting of *T. melanocephalum*. We observed many immature individuals drifting. Drift may also be an adaptation to the high mobility and population dynamics of *C. arenarium* and may facilitate to reach the same sites, especially in tidal waters. Because *T. melanocephalum* is able to perceive *C. arenarium* through the water, a certain density of drifting *C. arenarium* might be a trigger for *T. melanocephalum* to enter the water column as well. On the other hand, *T. melanocephalum* may just leave sites with low prey density by emergence. This may result in a density dependent response race between the predators and the prey over a large spatial scale. Thiel (1998) proposed to scale the predators' mobilities and foraging ranges before assessing their role rather than classifying them as epibenthic or endobenthic. *T. melanocephalum* has several mobility strategies with being more or less stationary in a certain area – leaving the sediment for foraging and retreating again during low tide – or drifting in the water column. For the prey, predictability of presence or absence of predators may be important in determining the attractivity of a locality for settling (Armonies, 1994). Thus, with respect to predator avoidance, the high intertidal is the most favourable zone for mobile *C. arenarium*.

Distribution of predator and prey

In sandflats, *T. melanocephalum* prefers the upper intertidal and lives in close association with *Corophium arenarium* (Gibson, 1995; this study). However, at a finer spatial scale within the upper intertidal, we found a maximum surface activity of *T. melanocephalum* at a transect site below that of maximum prey abundance. Limited time for capturing prey may be one factor preventing *T. melanocephalum* from exploiting the higher intertidal with highest prey densities. For searching food, *T. melanocephalum* depends on a thin film of water on the sediment surface. In summer 1994, we found an area with high *C. arenarium* density not submerged at all for about 30% of all tides. As a consequence, this upper zone may dry up quickly. Therefore, the availability of food for *T. melanocephalum* may not

be highest where prey was most abundant. The upper limit of both predator and prey was controlled by abiotic factors, but restricting *C. arenarium* less than *T. melanocephalum*.

In contrast, the lower limit of *T. melanocephalum* is most probably determined by prey density. In an area with naturally low density of *C. arenarium*, we found a strong invasion of nemertines into experimental plots with increased prey densities. This area is located about 20 cm below that of high prey density and was submersed more frequently: only about 10% of all tides did not reach this zone.

Another factor controlling *T. melanocephalum* distribution may be their dependence on burrows of *Nereis diversicolor* for accommodation (Bartsch, 1973). *T. melanocephalum* is not able to dig into the sediment itself and follows chemical cues of *N. diversicolor* (Bartsch, 1977). High on the shore *N. diversicolor* was scarce and we found an inverse relation of abundance between *N. diversicolor* and *C. arenarium*. Thus, *T. melanocephalum* faces a dilemma. Spatial separation of accommodation and food may result in the choice of an area where both are sufficiently available. Furthermore, *N. diversicolor* has a negative impact on *C. arenarium*. This polychaete may cause emigration of *C. arenarium* by disturbance (Jensen & André, 1993). However, Flach (1993) and Beukema & Flach (1995) did not find negative interactions between *C. arenarium* and *N. diversicolor* and stress the significance of *Arenicola marina* in determining the lower limit of both *C. arenarium* and *C. volutator*. Our results indicate that additional factors may control the lower limit of *C. arenarium*. In our study area, *A. marina* did not occur at mid tide level, but *C. arenarium* became scarce there nevertheless. There was no sharp boundary between dense assemblages of sediment stabilizers (tube-building invertebrates like *Corophium* spp.) and sediment destabilizers (burrowing invertebrates like *Arenicola*) as described by Woodin (1983). In summary, there may exist a 'ménage à trois' between *T. melanocephalum*, *C. arenarium* and *N. diversicolor*. *T. melanocephalum* feeds on *C. arenarium* and depends on *N. diversicolor* as a provider of accommodation. Both drive *C. arenarium* out of the sediment, whereupon *C. arenarium* may find refuge high on the shore with an upper limit set by abiotic constraints.

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