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RESEARCH ARTICLE

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Carrion-feeding on the sediment surface at nocturnal low tides by the polychaete *Phyllodoce mucosa*

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Abstract Harsh physical conditions in the intertidal zone are the cause of an ample amount of dead macroinvertebrates, which constitute a food source for carrion-feeders. In the European Wadden Sea, this trophic guild includes decapod crustaceans and fish when the tide is in, while during nocturnal low tides the polychaete *Phyllodoce mucosa* is attracted in large numbers by dead mollusks, crabs or worms on the sediment surface. Within 10 s worms emerged to the surface, crawled as far as 15 m on mucus trails towards the carcass, sucked in tissue up to one-third of their own weight, and then quickly retreated to below the surface. Abundance of *P. mucosa* was highest in the lower intertidal zone and winter. The seaward high abundance pattern, however, did not continue into the shallow subtidal. In summer, few were attracted during daytime or when the tide was in. However, up to 447 worms aggregated at a single crushed mussel within 20 min at dusk during low-tide exposure. This study suggests that during winter carrion-feeding is an important trophic niche on cold-temperate, intertidal mud flats occupied by a phyllodocid polychaete that is segregated in feeding time from most other scavengers and benefits from cold-sensitive benthic invertebrates.

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Introduction

Food webs often show some degree of redundancy, with more than one taxon occupying the same or overlapping niches (Cohen 1978). This may contribute to damped dynamics and sustainable functioning. It also may increase efficiency in the use of resources when spatial and temporal dimensions of combined niches are wider than individual niches. The trophic guild considered here is carrion-feeding on intertidal mud flats in the Wadden Sea, the shallow eastern coastal zone of the temperate North Sea, protected by a chain of barrier islands. The harsh physical conditions with desiccation events in summer and periods of frost in winter, tidal currents dislocating drifting invertebrates, storm surges exposing endobenthic bivalves or worms, all may supply carrion-feeders with more food in the intertidal zone than in adjacent deeper areas. In addition, mortality by biotic factors such as diseases, parasites and competition, by predators incompletely consuming their prey, or by events of anoxia caused by deposited algae may also provide carrion. Although this food source is likely to be, at times, of quantitative importance, it is usually not incorporated into coastal food web studies (i.e. Kuipers et al. 1981; Baretta and Ruardy 1988; Asmus et al. 1998). Usually carrion is consumed immediately by bacteria or animals; however, particularly in severe winters, the visible occurrence is very apparent. This may also be interpreted as a lack of consumer activity at times. When the tide is in, decapod crustaceans and fish are important carrion-feeders on tidal flats in the Wadden Sea. For example, during summer, we observed in traps baited with dead fish four times as many shore crabs (*Carcinus maenas*) as in unbaited traps (authors' personal observations). Eriksson et al. (1975a, 1975b) described shore crabs, shrimp and whelks as the dominant scavengers in Swedish shallow coastal waters. In the Wadden Sea, excavated infauna quickly attract shrimp (*Crangon crangon*) and gobies (*Pomatoschistus microps*) when the tide comes in.

At low-tide exposure, gulls and crows are observed picking on carrion. Common carrion-feeders on temperate to tropical shallow waters are nassariid gastropods (Yonge 1976; Tallmark 1980; Hurd 1985; Britton and Morton 1994; McKillup and McKillup 1997; Morton and Chan 1999). One of the most well-known grazers, *Littorina littorea*, may also scavenge animal tissue (Hayes 1929; Fenske 1997; Petraitis 2002). However, *L. littorea* is normally found on rocks and boulders along moderately sheltered upper shores covered with seaweeds. Furthermore, nassariid gastropods are not presently found in the Wadden Sea. Instead, we observed the agile polychaete *Phyllodoce mucosa* surfacing from dusk to dawn on flats exposed at low tide, crawling towards dead or injured mollusks, crabs, worms, or fish to feed on this carrion (Reise 1979a). Here, we describe by means of observation and experiments the mode of carrion-feeding by *P. mucosa*. The aim of the present study was to delineate the spatial and temporal niche of this common intertidal polychaete relative to other members of this neglected trophic guild.

Materials and methods

Study area

The study was conducted at Oddewatt, a tidal flat in southeastern Königshafen (about 1 km^2 in size), located at the northern end of the island of Sylt in the eastern North Sea (Fig. 1). Due to dune sand that is carried by winds into the intertidal area, the sediment is composed of medium-grained sands (median approximately 450 μm), in spite of the sheltered location. The area is within the cold-temperate region, with a mean annual water temperature of about 9°C (summer average of 15°C and winter average of 4°C). Tides are semidiurnal, with a mean range of 1.8 m. Salinity remains close to 30. The sediment surface of the upper area of Oddewatt (above −0.8 m mean tidal level; MTL) is scattered with fecal castings of the lugworm *Arenicola marina*, whereas the lower part of the flat (below −0.8 m MTL) is densely covered by sand tubes of the polychaete *Lanice conchilega* in most years. In between, there

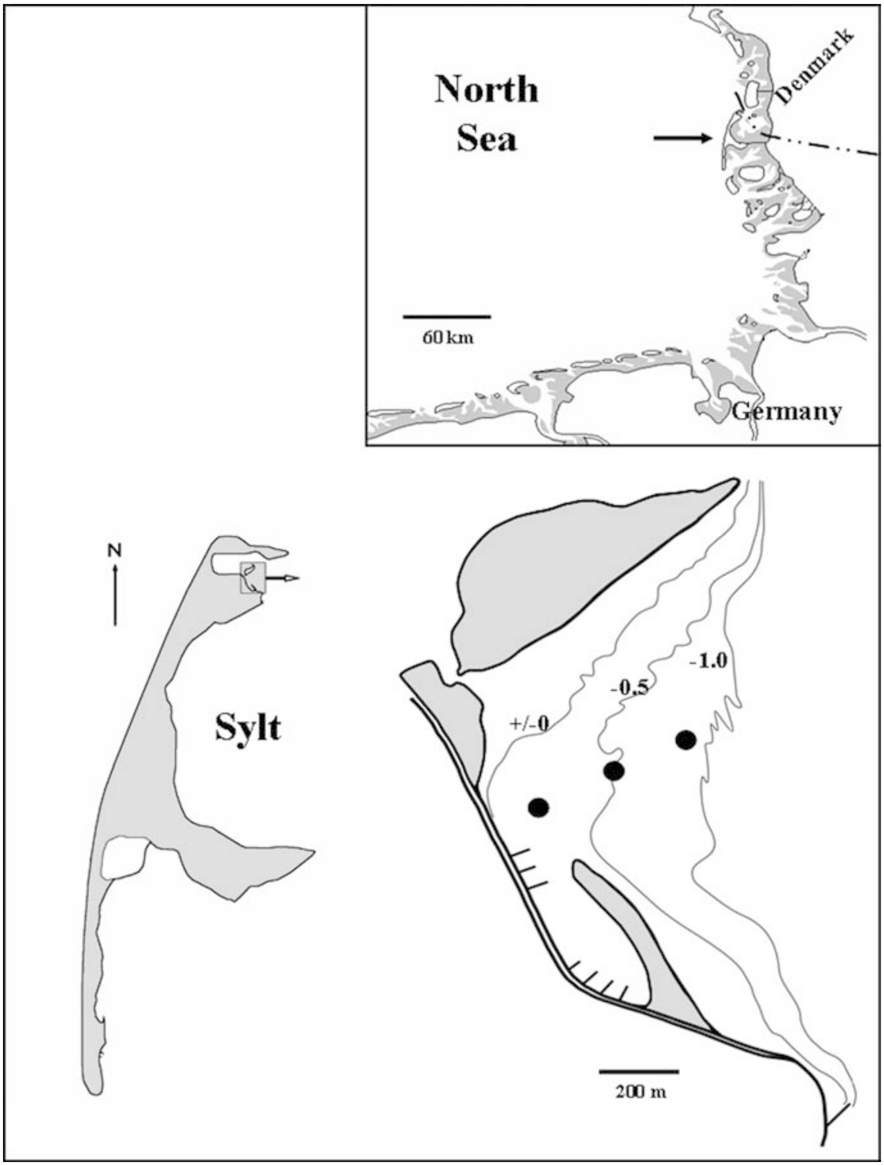

Fig. 1 Study area, Oddewatt, a tidal flat at the northern end of the island of Sylt in the North Sea [*filled circles* sampling stations; *isolines* depth (m) relative to mean tidal level, spring low-tide line at about −1.0 m]

are some remnants of former mussel beds. Further information on sediments and biota of the study area is given by Reise (1985), Armonies and Hellwig-Armonies (1992), Austen (1994), Reise et al. (1994) and Strasser and Pieloth (2001).

Taxonomy

Phyllodoce (*Anaitides*) *mucosa* (Oerstedt, 1843) has been occasionally synonymized with the similar *P. maculata* (Linnaeus, 1767). Gillandt (1979) referred to the presence or absence of a vertical rib on the dorsal cirri and the shape and length of the ventral cirri. She concluded that intermediates occur between the taxa and gave priority to the taxon named first. She also indirectly suggested that the study of Sach (1975) on the reproduction of *P.* Emphasis Type = "Italic" > mucosa on tidal flats in the Wadden Sea actually dealt with *P. maculata*. Hayward and Ryland (1990) suspect that *P. mucosa* may merely be a juvenile form of *A. maculata*. However, notwithstanding the intergrading of some characters, there seem to be consistent differences in pigmentation (Pleijel 1988; Hartmann-Schröder 1996), which we used to identify our material from the intertidal flats near Sylt as *P. mucosa*. The anterior part of the prostomium is pigmented brown, and on the ventral side, the first segment behind the mouth is brownish as well. In *P. maculata* the prostomium is not pigmented brown, and dorsally, but not ventrally, the first two segments behind the peristomium are brownish. Earlier records from tidal flats near Sylt (i.e. Wohlenberg 1937; Smidt 1951) and presumably also from other tidal flats in the Wadden Sea are likely to belong to *P. mucosa* and not *P. maculata*. From the photographs published in Sach (1975), the specimen appears to be *P. mucosa*. Genetic studies have not yet been conducted to solve this question.

Distribution

A transect was established at Oddewatt, from the dike towards the low-tide line, with sampling stations at −0.3, −0.5 and −0.8 m MTL. At each station, five sediment samples were taken using a box corer (225 cm^2, 20 cm depth) during low tides in April 2002, washed gently on a 0.5-mm-mesh sieve, and then the number of retained *P. mucosa* was counted. At approximately the second station of the transect, the abundance of *P. mucosa* was estimated by M. Huettel with a cylindrical corer (24 cm^2, 13 cm depth) and a 0.25-mm mesh, replicated six times at each of six dates in the period from August to December 1983.

Size, weight and consumption

To measure the length of *P. mucosa*, 107 individuals were collected with bait and made to crawl through a glass capillary placed on graph paper. Crawling speed was measured through a 1-m silicon tube with 20 worms. Wet weight was determined after removing mucus on blotting paper. The amount of mussel (*Mytilus edulis*) meat consumed was estimated by supplying each of the 40 petri dishes (140 mm diameter) with seawater and with about 100 mg of mantle tissue. Half of the set of petri dishes received ten *P. mucosa* of adult size (22–35 mg), previously kept without food for 2 days. After 2 h, when all worms had stopped feeding, the mussel tissue was weighed again. Average weight loss of mussel tissue in petri dishes without worms was 5 mg. This weight loss was subtracted from the weight loss found in the petri dishes containing *P. mucosa*.

Food choice experiments

P. mucosa was tested to see if it is a potential predator on juvenile macrofauna settled on tidal flats. Seven petri dishes (90 mm diameter) were provided with azoic sand and natural seawater. In each dish, ten *P. mucosa* were kept for 2 days at room temperature without food. Then, ten live individuals of each potential prey (juvenile polychaete *Scoloplos armiger* and *Typosyllis hyalina*; bivalve spat of *Cerastoderma edule*, *Ensis americanus* and *Macoma balthica*; crustaceans Ostracoda and Copepoda) were offered and counted at intervals over a period of 5 days. Prey organisms were collected at Oddewatt from the upper 2 cm of sediment with a 0.25-mm mesh in spring (April–June). *P. mucosa* was collected using crushed mussels as bait.

Offering bait

Attractivity was measured as the number of *P. mucosa* attracted to its food. Six fresh mussels were opened with a knife and placed randomly on the tidal flat surface with a minimum interval of 20 m between mussels. As soon as we put the mussels on the sediment, *P. mucosa* gathered at the mussels. After 20 min, each area bearing mussel that had attracted *P. mucosa* was sampled using a circular corer of 200 cm^2. This experiment was conducted during diurnal and nocturnal low tides in June 2002 and also when the tidal flat was submerged by the flooding tide at 15–20 cm water depth. In the latter experiment, one set of mussels was also covered by 5-mm-mesh cages in order to prevent any interference from visiting carnivores such as shore crabs (*Carcinus maenas*) and brown shrimps (*Crangon crangon*). For statistical analysis, the attractivity values were compared using a *t*-test after variance homogeneity was tested with an *F*-test.

Results

Distribution, abundance and size

Phyllodoce mucosa mainly occurred in the lower intertidal zone. About 90% of all *P. mucosa* were found below −0.5 m MTL in April 2002 (Fig. 2). Average abundance of *P. mucosa* was 110–260 individuals m^{-2} around mid-intertidal (−0.3 to −0.5 m MTL) and increased to 700 individuals m^{-2} at low-tide level (−0.8 m MTL), particularly where sand tubes of the polychaete *Lanice conchilega* were dense. This seaward high abundance pattern, however, did not continue into the shallow subtidal. Strong easterly winds that caused extreme low tides allowed us to occasionally sample the area down to −1.5 m MTL. Here, the average abundance of *P. mucosa* was only 100 individuals m^{-2}.

Sampling from August to December 1983 revealed an increasing abundance from summer to winter (Fig. 3).

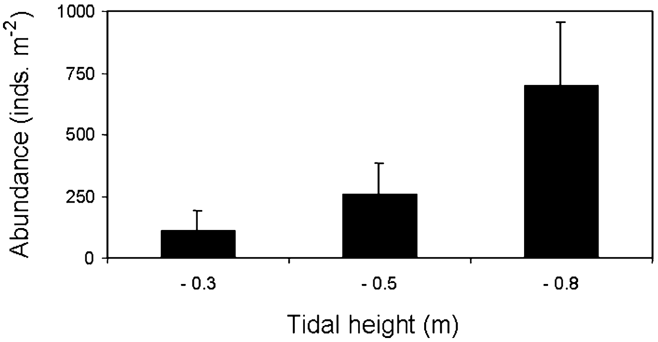

Fig. 2 *Phyllodoce mucosa*. Abundance (+SD, m^{-2}) in relation to tidal height at Oddewatt, April 2002

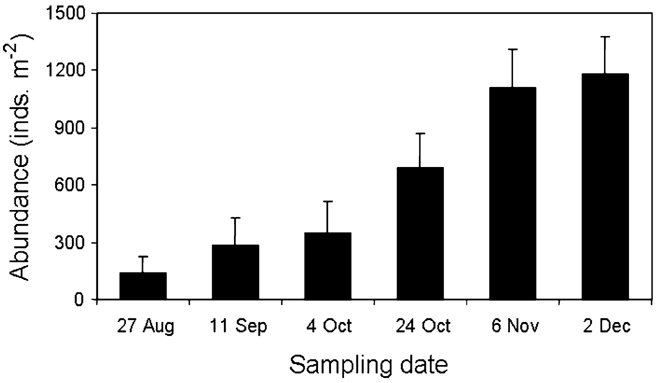

Fig. 3 *Phyllodoce mucosa.* Abundance (+SD, m^{-2}) at −0.5 m below mean tidal level at Oddewatt from August to December 1983, measured with six cores of 24 cm^2 (13 cm depth) at each date

Abundance reached 1200 m^{-2} in December. The length of the polychaetes collected ranged between 40 mm (8 mg) and 105 mm (31 mg), with worms around 70 mm (18 mg) being the most common (Fig. 4).

Feeding behavior

In summer, *P. mucosa* may be observed at the sediment surface from dusk to dawn during low-tide exposures. On cloudy days, and from autumn to spring, some worms also show up on the sediment surface during diurnal low-tide emersion. When placing a dead shore crab within a metal frame of 0.25 m^2, *P. mucosa*, concealed in the sand within the enclosed area, appeared at the sediment surface after 10 s (average of 20 measurements). When at the surface, worms straddle their tentacles and slightly lift and swing their anterior end, presumably to locate the source of the olfactorial clues.

When the receding tide left only a thin film of water on the tidal flat, the distance from which worms approached a dead crab reached maximum values, up to 15 m or approximately 200 times its body length. For such a distance, *P. mucosa* may need some 40 min to crawl. On average, 20 worms crawled through a 1-m silicon tube in 2.5 min. *P. mucosa* massively secretes mucus when crawling, and conspecifics tend to follow existing trails, sometimes forming "roads" with several parallel trails directed towards a carcass. No interference between worms aggregating at a common food source was observed.

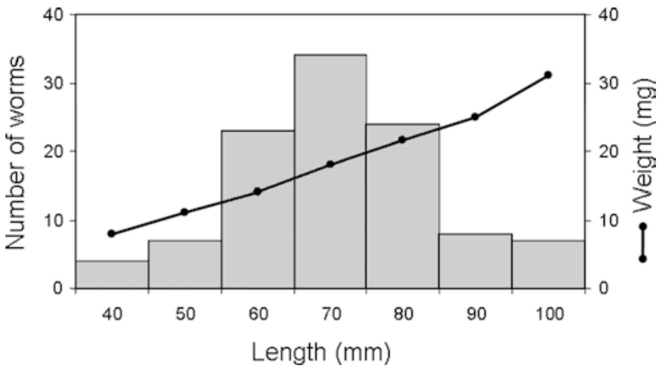

Fig. 4 *Phyllodoce mucosa.* Length frequency and wet weight (*line*) of 107 individuals collected on 27 October 1983 at Oddewatt

On arrival at a corpse, which may be a dead mollusk, lugworm, crab, or fish, the muscular pharynx is everted (see Fig. 8), and tissue is sucked in by peristaltic movements accompanied by continuous mucus secretion. Most worms seemed to be satiated after 20 min; by then all feeding ceased. Our feeding experiment suggests that an adult worm of 31.4 mg consumes, within 20 min, up to 9.1 mg of mussel tissue, corresponding to 29% of its own weight. Average figures from 20 replicates each with ten worms in petri dishes are: individuals of 28.6 ± 3.5 mg consumed 4.7 ± 2.3 mg, corresponding to 16% of their own weight.

Eat-and-run behavior

When crushed mussels were placed on the sediment surface, *P. mucosa* gathered at the carrion and we expected the number of attracted worms to increase over time. However, only a small portion of the worms remained at the carcass although much food was left. In a field experiment, the number of *P. mucosa* after 20 min was almost threefold compared to that after 60 min ($t_{10}=2.6$, $P=0.014$; Fig. 5). Once *P. mucosa* spots the food on the sediment surface, they quickly approach, suck from the carrion several times, and then move away from the food source. This behavior may protect them from becoming prey to larger carnivores (e.g. shore birds) that are also interested in the carrion.

Only scavenger or also predator?

Our choice experiments showed that *P. mucosa* does not seem to prey on mobile invertebrates. In the laboratory,

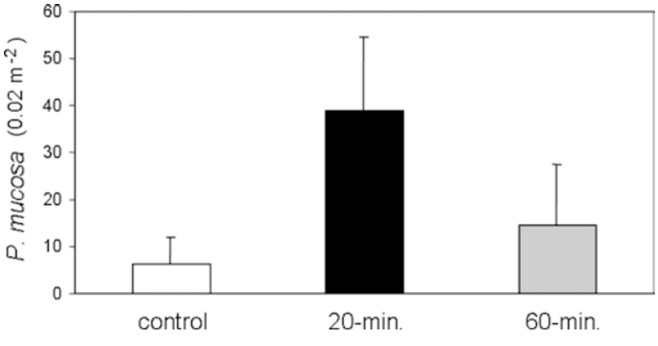

Fig. 5 *Phyllodoce mucosa.* Average number (+SD) attracted to a crushed mussel after 20 min and 60 min in Oddewatt, in June 2002. Due to rapid feeding and retreat, the number of worms after 60 min was less than after 20 min ($t_{10}=2.6$, $P<0.05$)

we put ten worms into each of two petri dishes and supplied them with ten living juvenile polychaetes, *Scoloplos armiger* or *Typosyllis hyalina*. During 5 days of observation, none of the prey was eaten by *P. mucosa*. However, when we provided them with the same but dead specimens killed by freshwater shock, all of the prey was swallowed by *P. mucosa* within 10 min. We continued to feed the worms with other potential prey such as live bivalve spat of *Cerastoderma edule*, *Ensis americanus* and *Macoma balthica* and the crustaceans Ostracoda and Copepoda, but again those were not eaten by *P. mucosa*. On the other hand, the living tissue of freshly crushed mollusks is a highly desirable food for *P. mucosa* and injured but living polychaetes (*Heteromastus filiformis*) that lost their motility are also consumed immediately.

Nocturnal carrion-feeding

Close examination of the tidal flat surface at dusk revealed that many *P. mucosa* emerge from the sediment and feed in low-tide puddles. Such emergences were rarely observed during daytime and never during bright sunshine. In two sets of experiments, *P. mucosa* was about eight times more abundant at crushed mussels provided during dusk than in daylight, exposed for 20 min on the sediment surface ($t_{10}=6.7$, $P<0.001$; Fig. 6). The mean number of attracted worms in daylight was 39 individuals (range: 21–64 individuals per 200 cm^2; $n=6$), whereas it was 302 individuals at dusk (range: 233–447 individuals per 200 cm^2; $n=6$). This result shows that the foraging and feeding activities of *P. mucosa* on exposed intertidal flats preferentially take place during night time.

Tidal pattern of feeding behavior

During nocturnal low tides, *P. mucosa* was seen crawling on the sediment surface until just before the next incoming tide. They buried themselves in the sediment as the flooding tide covered them. When the sediment was submerged by up to about 20 cm of water, we tried to attract *P. mucosa* with mussel carrion but failed. There was no significant difference in the number of worms between treatment and control ($t_{10}=-0.6$, $P>0.05$; Fig. 7). Instead of *P. mucosa*, many shore crabs (*Carcinus maenas*) and brown shrimps (*Crangon crangon*) fed on crushed mussels. Even when protecting the offered carrion with cages from these carnivores, there was no significant gathering of *P. mucosa* ($t_{10}=-0.7$, $P>0.05$; Fig. 7). This indicates that nocturnal activity of *P. mucosa* is restricted to low tide and that the polychaetes are less active on the sediment surface during high tide.

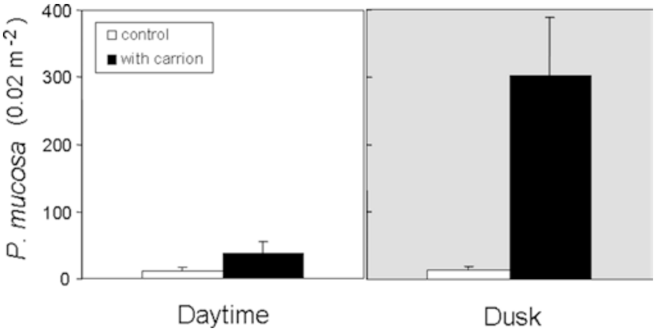

Fig. 6 *Phyllodoce mucosa*. Attractivity during daylight and dusk. Attractivity was measured as the number of individuals (+SD) attracted to a crushed mussel after 20 min on a tidal flat, Oddewatt, in June 2002

Discussion

Adults only in the intertidal zone?

Due to the ambiguity as to whether published reports refer to *Phyllodoce maculata* or *P. mucosa*, not much is known for certain about the distribution, abundance and life history of *P. mucosa*. As described by Sach (1975), greenish spheroid egg cocoons, each fixed with a stalk to the sediment, are produced nocturnally between February and May. From these, pelagic larvae hatch, but do not seem to settle in the intertidal zone. Almost all individuals we found on the tidal flats were longer than 40 mm. The increase in abundance observed from summer to winter may reflect dispersal of young worms from the subtidal into the tidal zone. High numbers of adult *P. mucosa* during winter were recurrent throughout the last two decades in the study area. This pattern, with juveniles in subtidal and adults in intertidal locations, contrasts with the often noted nursery function of tidal flats for flatfish, shrimps and shore crabs, which, as adults, retreat to the subtidal zone (Reise 1985), or with lugworms (*Arenicola marina*: Farke et al. 1979; Reise et al. 2001), king rag worms (*Nereis virens*: Miron and Desrosiers 1990) and the tellin *Macoma balthica*

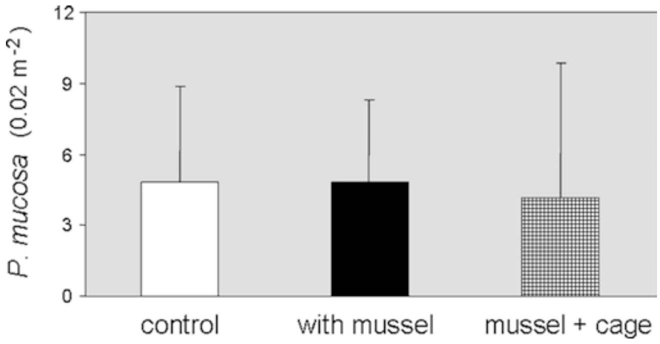

Fig. 7 *Phyllodoce mucosa*. Attractivity after being covered by the nocturnal flood tide in June 2002. Attractivity was measured as the number of individuals (+SD) attracted to a crushed mussel after 20 min on a submerged tidal flat, Oddewatt, having about 20 cm water depth. Cages excluded flood-tide visitors like crabs and shrimps

(Armonies and Hellwig-Armonies 1992; Beukema 1993), which use the upper tidal zone as a nursery.

Coldness supplies carrion

The inverse pattern of *P. mucosa* may be explained by abundant carrion on tidal flats in the cold-temperate climate zone caused by frost during winter (Smidt 1951; Crisp 1964; Beukema 1979; Reichert and Dörjes 1980). In years with severe frost, entire tidal populations of cold-sensitive species have been observed to die in the study area, i.e. the cockle *Cerastoderma edule* (Strasser et al. 2001) or the polychaete *Lanice conchilega* (Strasser and Pieloth 2001). The abundance of *P. mucosa* with $>1000\ \mathrm{m}^{-2}$ reported for Oddewatt in December is almost an order of magnitude higher than given for other tidal flats in other seasons (i.e. Hauser 1973; Reichert and Dörjes 1980; Michaelis 1987; Beukema 1991; Reise et al. 1994), which may simply reflect that sampling was rarely performed in the middle of winter. However, an increasing abundance of *P. mucosa* from summer to autumn was also noted by Hauser (1973), Reise (1978) and Reise et al. (1994). The cold-adapted *P. mucosa* takes advantage of the high mortality of cold-sensitive species coexisting on the same tidal flats in the North Sea.

The higher abundance of *P. mucosa* on tidal flats in winter compared to summer may not only be an adaptation to a higher supply of carrion, but to the segregation from crabs, shrimp and fish, which are all absent or rare in the tidal zone during winter (Creutzberg and Fonds 1971; Klein-Breteler 1976; Beukema 1992). We observed *P. mucosa* crawling between ice-floes and at water temperatures of -1°C or less. It appears that carrion-feeding in winter offers a niche with few competitors and predators in the Wadden Sea.

Dining at nocturnal low tides

The nocturnal low-tide activity of *P. mucosa* is a parallel to that of the nemertines *Lineus viridis* and *Amphiporus lactifloreus* occurring on the same tidal flats (Thiel et al. 1996). Although these are predators (Thiel and Reise 1993) and *P. mucosa* is mostly a scavenger, a common advantage may be that chemical cues lead them more readily to their food source in a thin film of water than during high tide with a comparatively large and well-mixed water mass. The fact that *P. mucosa* does not react to carrion submerged in deeper water may be due to a dilution and dispersion effect. In the oscillating flow that dominates in shallow waters, the orbital wave motion of the water leads to a rapid dispersion of odors, which makes it more difficult for the polychaete to track an odor plume (Black and Oldman 1999). The orientation in an odor gradient in deeper water may still work on a larger scale and guide the polychaetes that settled in the subtidal towards the intertidal flats. For *P. mucosa* low-tide exposure also implies a relief from predation or competition with scavenging crustaceans and fish. Our experiment with bait offered when the tide was in failed to attract *P. mucosa*. This indicates the existence of a specific adaptation to low-tide conditions, and one may wonder what *P. mucosa* feeds on in the subtidal zone. Nocturnal activity may be an adaptation to avoid UV-radiation. Solar radiation leads to the formation of oxygen radicals and peroxide, a cytotoxic agent permeating cell membranes, at the sediment–water interface (Halliwell and Gutteridge 1986; Szymczak and Waite 1988). Adult *P. mucosa* directly exposed to environmental hydrogen peroxide (H_2O_2) need to increase antioxidant enzyme (catalase) levels in their tissues for protection (Abele-Oeschger and Oeschger 1995). On the other hand, thin layers of sediment effectively attenuate UVA and UVB radiation by an order of magnitude (Ahrens and Hickey 2002). Thus, it may be beneficial for the worms to stay in the sediment during bright sunshine, avoiding energy expenditure on antioxidant enzyme production. The observation that on cloudy days and from autumn to spring, some *P. mucosa* show up on the sediment surface during diurnal low-tide emersion is in line with this interpretation. Whether subsurface food sources are of any quantitative importance is not known. Carrion placed below the sediment surface is also exploited by *P. mucosa*. However, larger pieces of carrion within the sediment will soon give rise to anoxic and sulfidic conditions in the sediment, probably preventing any further exploitation by an oxibiotic polychaete.

Predators

Crabs, shrimp and fish may not just be competitors to *P. mucosa*, but predators as well. Preliminary experiments in the laboratory revealed that gobies (*Pomatoschistus microps*), shrimp (*Crangon crangon*) and hermit crabs (*Pagurus bernhardus*) do prey on *P. mucosa*, although other polychaetes (*Capitella capitata*, *Scoloplos armiger*, *Eteone longa*) were preferred. The shore crab *Carcinus maenas* captured *P. mucosa*, but let it free again, while other polychaetes were eaten. This may be important because shore crabs are also active on the tidal flats during nocturnal low tides. Presumably, *P. mucosa* gets some protection from the mucus it produces in masses. It is not known whether birds pick at *P. mucosa*. However, the nocturnal activity of the worms and their rapid retreat below the surface after a quick meal may help to conceal them from visual hunters. *P. mucosa* readily burrows through sand, but also uses burrows or tubes of other infauna (i.e. tubes of *Lanice conchilega*) to retreat from the sediment surface.

Exclusively a carrion-feeder?

Gravier (1896) and Sach (1977) note that during the spawning period (February–May) the body is mostly

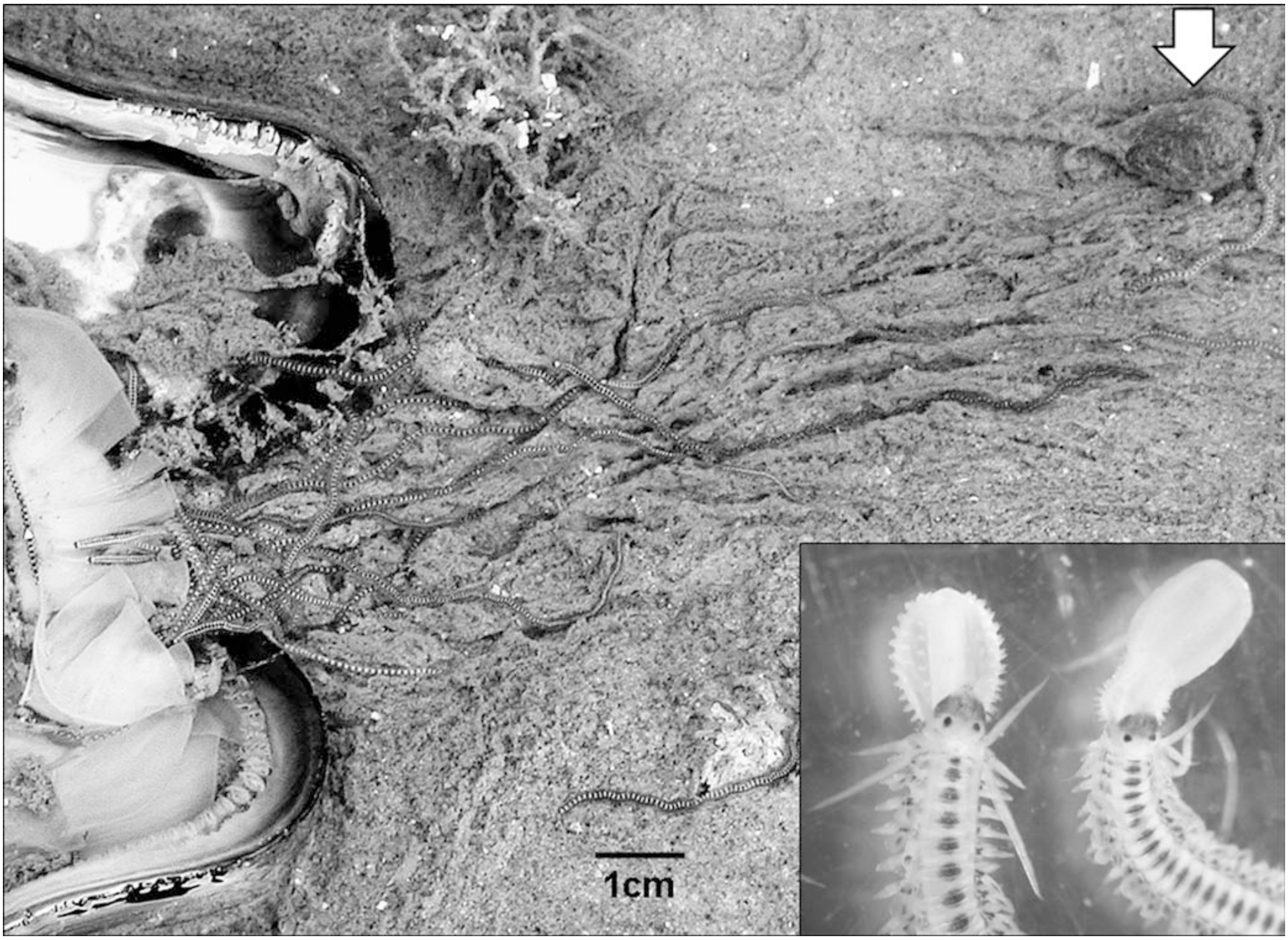

Fig. 8 *Phyllodoce mucosa*. Active scavenging on a mussel (*Mytilus edulis*) during the spawning period (egg cocoon is indicated by an *arrow*). *Inset*: a close-up of the anterior end, with an eversible pharynx

filled with gametes, the gut is squeezed and muscles may be reduced. Thus, they conclude that food cannot be taken up during this period. However, we observed that the scavenging of *P. mucosa* continued under field and laboratory conditions throughout the spawning period (Fig. 8). Phyllodocidae are generally considered carnivores (Fauchald and Jumars 1979), and Hartmann-Schröder (1996) described *P. mucosa* as a predator on small invertebrates, including small conspecifics. A field experiment near Sylt also indicated that small macrofauna (juvenile *Hydrobia ulvae* and annelids < 30 mm in length) were reduced in number by enclosed *P. mucosa* (Reise 1979b). Our experiments in the laboratory, however, suggested that adult *P. mucosa* do not attack motile prey. We also found no evidence for cannibalism. Either the potential diet of the species on the whole is more diverse than that realized by carrion-feeding (present study), or earlier reports apply to *P. maculata* and not to *P. mucosa*. On the other hand, we have little knowledge concerning the food taken by benthic juveniles < 40 mm in length, by worms burrowing within the sediment, and by subtidal worms. Further investigations are required.

Carrion-feeding on tidal flats

In food webs, the terms "predators" and "carnivores" are often used as synonyms. However, it is only the latter that includes carrion-feeding. Many carnivores are both, predators and scavengers, and a clear distinction is not always possible. Fauchald and Jumars (1979) in their review on the diet of polychaete worms mention carrion-feeding for members of the Amphinomidae, Eunicidae, Lumbrineridae, Onuphidae, Phyllodocidae and Syllidae, but conclude that the distinction from predation is usually impossible in practice. There may be considerable coincidental or optional carrion-feeding, while obligatory scavenging may be less widespread in the marine benthos. Adult intertidal *P. mucosa* may be an example for dominant carrion-feeding by a polychaete.

On tidal flats, some nassariid whelks are obligatory carrion-feeders (Brown 1961, 1982), and one of these, *Hinia* (*Nassarius*) *reticulatus*, once occurred in the tidal zone around Sylt, including Oddewatt at the low-tide level (Reise 1982; E. Ziegelmeier, personal communication). It may have almost vanished in the wake of an eelgrass disease in the 1930s, but lingered on until the 1960s. *P. maculata* (=*mucosa*?) was reported to be rare at the time of *N. reticulatus* (Wohlenberg 1937). Maybe there was more competition for carrion than at present, as this whelk is also nocturnal in feeding activity, although it becomes inactive in cold winters (Eriksson and Tallmark 1974).

Apart from special events, freezing temperatures in winter may be the most important mortality factor leaving carrion on the tidal flats in the North Sea. Exploiting this winter resource may allow *P. mucosa* to partition much energy into reproduction in the spring time. In other regions, for example, monsoon seasons or humans digging for specific clams are likely to be more important on tidal flats for providing carcasses of benthic fauna. Without carrion-feeders this food source might be washed away with the tides and would, thus, be lost from the nearshore food web. However, quantitative work on this component is still to be done.

Conclusions

The realized trophic niche of *P. mucosa* on tidal flats is shown to be that of a carrion-feeder. It avoids competitors and predators by crawling and feeding at the sediment surface during low-tide exposure, from dusk to dawn, and particularly exploits carrion during winter, when mortality in other benthic invertebrates is high in the tidal zone of the Wadden Sea. High crawling speed, mucus trailing (as a mutual benefit to conspecifics leading to the food source) and the ability to locate a carcass from a distance, all may contribute to the success of *P. mucosa* as a carrion-feeder. The apparent redundancy within the functional group of carrion-feeders is spurious. Without *P. mucosa*, carrion, in winter, would be lost for benthic invertebrates of the tidal sediments.

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