Meiofaunal emergence from intertidal sediment measured in the field: significant contribution to nocturnal planktonic biomass in shallow waters

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ABSTRACT: Field studies on the occurrence of meiobenthos in the water column above intertidal sandflats have been performed near the Island of Sylt in the northern Wadden Sea. Swimming meiobenthos was strongly dominated by harpacticoid copepods. Many of them have a semiplanktonic life-style. They rest in superficial sediment layers at low tide and swim in the water column at high tide. Swimming activity correlated negatively with light. The abundance in the water column was one order of magnitude higher during the night. Strong currents caused by storm tides significantly decreased meiobenthic abundance in the water column. Light and flow being constant, no significant changes of meiobenthic abundance per unit area occurred over a tidal cycle. Since holoplankton and meroplankton abundances correlated positively with the height of the water column, semiplanktonic meiobenthos may dominate the mesozooplankton in shallow waters. On an average, emergence of meiobenthos increased the mesozooplanktonic biomass by about 2 % during diurnal high tides over the entire tidal cycle, and by about 50 % during nocturnal high tides. Because of seasonal cycles of the dominant harpacticoids, this high contribution to planktonic biomass may be a summer phenomenon.

INTRODUCTION

Traditionally, meiobenthos was thought to be confined to either living in the sediment or its interstices, or performing an epibenthic life-style with intermittent hiding in the sediment. However, recent investigations revealed that at least some meiofaunal taxa may actively leave the sediment and swim in the water column (Alldredge & King, 1977; Hobson & Chess, 1979; Hammer, 1981; Sibert, 1981; Ohlhorst, 1982; Hicks, 1986; Walters & Bell, 1986; recently reviewed by Palmer, 1988). Most of these studies deal with tropical to warm temperate subtidal habitats. Laboratory experiments on the emergence behaviour of boreal intertidal meiobenthos (Armonies, 1988a, b, c) yielded the following predictions: (1) Copepoda and Plathelminthes may actively enter the water column; Ostracoda perform an epibenthic life-style, and Nematoda, Gastrotricha and Oligochaeta seem to live endobenthically. (2) The copepod and plathelminth swimming activity correlates negatively with light, i.e. their abundance in the water column should be higher during nocturnal than during diurnal high tides. (3) Currents affect the abundance of active swimmers in the water column. Abundance should be highest at weak currents, decrease as currents become stronger, and increase again when the sediment becomes eroded. In the latter case, Nematoda, Gastrotricha and Oligochaeta should also be found

in the water column. (4) The swimming activity of harpacticoid copepods and plathelminths is also affected by physical factors such as temperature, salinity, and oxygen. However, the effects of these factors seem to be species-specific and in most cases there is no general pattern. The potential benefits and risks of active swimming in the water column are discussed by Alldredge & King (1980, 1985) and Armonies (1988a, c).

The present study combines field sampling in the water column and sediment to test for (1) the presence of active swimmers in the water column above boreal intertidal sandflats, (2) a light effect, and (3) a decrease in swimming activity during periods with stronger currents. (4) Another aim of this study is to quantify the contribution of swimming meiobenthos to the biomass of mesozooplankton.

MATERIAL AND METHODS

Study sites and sample collection

Meiobenthic emergence into the water column was studied at the extensive tidal flats of the Königshafen wadden area near the Island of Sylt in the North Sea. For a general description of the area see Reise (1985). Three sites were sampled between July and September 1988 (Fig. 1): (1) Site I was a 20 × 20 m square of a sheltered sandy tidal flat NE of the village of List. The sediment was mainly composed of fine sand (median diameter 150 μm, sorting coefficient 1.5). During an average tidal cycle, this site was submerged for 4 h (approx. 33 %) and the average height of the water column at high tide was 0.6 m. (2) Site II was a 40 × 10 m plot of medium sand (median diameter 324 μm, sorting coefficient 2.46) north of the village of List. The average submergence was 8 h per tidal cycle (approx. 66 %) and the average high water level was 1.1 m. (3) Site III marks a series of 10 locations extending from site I to site II (distance approx. 300 m of shoreline) and further west to the Lister Haken. The total distance of shoreline covered by the 10 locations was about 600 m, and individual locations were at least 50 m apart. The granulometric composition of the sediment varied from fine sand (site I) to coarse sand near the Lister Haken. The height of all locations was as at site I (i.e. about 33 % of tidal submergence).

Sediment samples were collected at low tide using glass tubes of $1 \, cm^2$ inserted into the sediment to a depth of 2 cm, thus only covering the brownish superficial sediment layers. Each set of both sediment and water samples consisted of at least 10 replicates. Three methods were applied to collect seawater samples above the intertidal sandflat. (1) Pipe samples were collected by vertically inserting plexiglas pipes of $10 \, cm^2$ and variable length (0.3, 0.5, 1.0, 1.5 m depending on the water depth) into the water column down to a few centimetres above the sediment. The pipe was closed with a rubber stopper at the upper end and withdrawn until the lower end was just below the water surface. The lower end was closed and then the pipe removed from the water. Such sampling yields a water column of $10 \, cm^2$ surface area reaching from the water surface to some cm above the sediment. Samples containing sand grains (by contact with the sediment surface) were rejected. To avoid artificial suspension of sediment and associated meiofauna, pipe samples were collected from a rubber dinghy which glided along a cable anchored at the sample site and the shore. The dinghy was pushed by hand along the cable, thus no oars or paddles disturbed the water layer or sediment surface. The cable also helped our
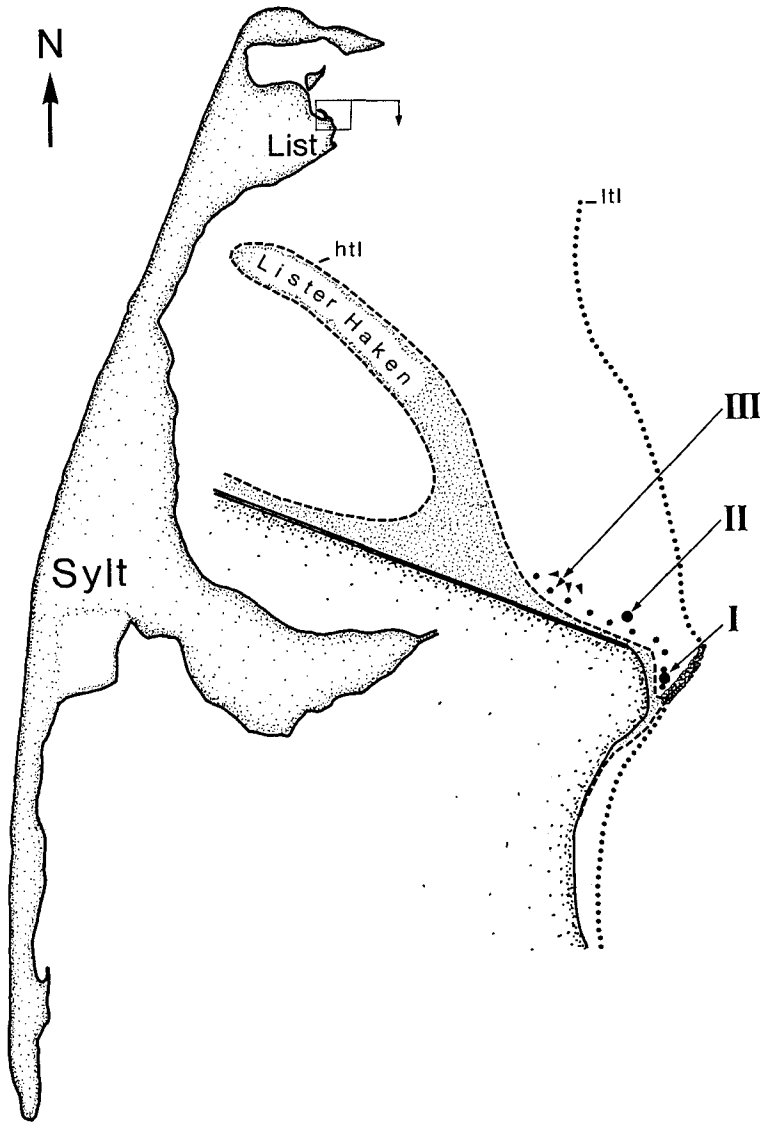
Fig. 1. Position of sampling sites (I, II, III) off the Island of Sylt in the northern Wadden Sea. htl = high tide level, ltl = low tide level

return to the same locations in the case of repeated sampling during the tidal cycle (see below). (2) Samples of surface water were collected by scooping with a $12\,dm^3$ bucket with a rectangular opening (top 30 cm of the water column). (3) A $64\,\mu m$ plankton net with the opening fixed to a rectangular frame of $20 \times 40\,cm$ was mounted onto a sledge to sample the water column horizontally between 10 cm (position of the lower opening of the frame above the sediment) and 50 cm above the sediment. A 12.5 m tow of this net

filters $1 m^3$ of seawater. Such a sample from site II was used to estimate the individual biomass values of various taxa (see below).

Water samples were sieved through 63 μm meshes and the remainder returned to the laboratory. The sediment and net samples were immediately preserved in 5 % formalin. From the other water samples, animals were sorted alive using a dissecting microscope, and hard bodied meiofauna was subsequently preserved in 5 % formalin for later counting and identification. All metazoan taxa except copepod nauplii (harpacticoid as well as calanoid) were counted but specimens that were retained on a 500 μm sieve (e.g. shrimps, brachyuran megalopae) were excluded from later analysis.

Testing for diurnal differences of meiobenthic emergence

At site III, a $10 dm^3$ sample of surface seawater was scooped from each of the 10 locations, once during daytime at high tide (August 27th), and once during the succeeding nocturnal high tide (August 28th). Abundance of the various taxa in the water samples is compared by Wilcoxon's matched pair signed rank statistic applied to the diurnal and nocturnal samples in each of the 10 locations. During the daytime sampling, the wave height was 5 cm in the most sheltered and up to 15 cm in the most exposed locations. There was less wind during the night and the wave height was mostly below 5 cm with a maximum of 10 cm at one location.

Influence of strong currents

Laboratory experiments suggest decreased abundance of semiplanktonic species in the water column as flow increases above a current speed of approx. $1 cm \cdot s^{-1}$ (Armonies, 1988b; current speed measured 1 cm above the sediment surface). At the Island of Sylt, westerly gales greatly increase the current speed in the Wadden area and increase the high tide level. Water samples of $1 dm^3$ volume (pipe samples from the top 1 m of the water column) were collected during two nights with westerly storms (September 11th, n = 24, and September 12th, n = 20) at site II. Abundance of the various taxa was compared with the daytime water samples of September 8th, collected at the same site with the same method (n = 24) but during periods where there were only slight winds. In all cases, sample collection started 1 h after highest water level (falling tide). On September 8th (daytime), the water level did not significantly differ from the average (1.0 m, 1 h after high tide). The surface current speed was about $10 cm \cdot s^{-1}$ (measured by drifting objects). During the stormy nights, the tidal height was increased to 1.3 and > 1.5 μm, and the surface current velocity was about $0.5 m \cdot s^{-1}$ and $0.8 m \cdot s^{-1}$ on September 11th and 12th, respectively.

Quantification of meiobenthos in the water column

This was done using pipe samples of the entire water column from a rubber dinghy. Each of the seawater samples at each of the sampling dates consisted of 10 replicate water columns collected at least 2 m apart over a total distance of 20 m (site I) or 30 m (site II). In the July samples, each of the replicates was separately transferred into plastic bottles while the 10 replicates of the August and September samples were pooled.

Depending on the actual height of the water column, the volume of collected seawater varied between 0.7 and 12 dm^3 per 10 replicates. There were 5 sampling occasions: (1) July 10th, 2 h before nocturnal high tide (= ht − 2 h), at site II; (2) July 12th, daytime, site I, ht − 2 h, ht − 1 h, ht + 1 h, ht + 2 h; (3) July 13th, nighttime, site I, ht − 2 h, ht − 1 h, ht + 1 h; (4) August 8th, nighttime, and (5) September 9th, daytime, site II. Nineteen sampling dates distributed over the entire tidal cycle: at first, 6 samplings were carried out at 15 min intervals, starting 15 min after the sample site had been reached by the incoming tide; then, at 30 min intervals until the tide left the site again (see Figs 1, 2, 3). Light, air and seawater temperature, tidal height, and wave height were monitored at the same intervals.

Biomass estimation

A 64 μm plankton net sample from site II (August 11th) was used to determine the average individual dry weights of the dominant zooplankters and meiobenthic taxa, following the procedure described by Widbom (1984) for formalin-preserved specimens. These determinations for the more abundant taxa, and literature data from Widbom (1984), Hickel (1975), and Faubel (1982) were fitted according to the actual percentages of size classes in the above net sample and thus yielded the following average individual dry weights (all in μg) used for biomass calculation: holoplanktonic Appendicularia and Chaetognatha 1.0, calanoid copepods 1.5 (including copepodites but excluding nauplii), planktonic Plathelminthes 1.0, Rotatoria 0.2 (estimate); meroplanktonic taxa, nectochaeta larvae and barnacle nauplii 0.3, barnacle cypris larvae 3.0, spionid larvae 5.0, juvenile (5 to 6-setiger) *Arenicola marina* L. and trochophore larvae 1.0; semiplanktonic harpacticoids 0.8 (including copepodites but excluding nauplii), cyclopoids 0.3, plathelminths 1.0; benthic Ostracoda 2.0, Nematoda 0.5, and Plathelminthes 1.0 (all μg DW).

Statistical analysis·

Abundance data of both meiobenthic and planktonic taxa frequently deviated from a normal distribution (significant deviation of the variance-to-mean ratio from the appropriate reference of a chi-square table, p = 0.05, Gage & Geekie, 1973). In some cases, the 10 replicates forming a sample were pooled and thus no information is available on the between-replicate variation of abundances. Therefore, only non-parametrical methods are used: Wilcoxon's matched pair signed rank statistics, U-test (Wilcoxon et al., in Sachs, 1984), and Spearman's rank correlation coefficient (abbreviated by "r_s"). Significant results are indicated by * (p < 0.05), ** (p < 0.01) and *** (p < 0.001), respectively.

RESULTS

Diurnal differences in the composition of mesozooplankton

The daytime zooplankton above intertidal sandflats of the Wadden Sea is strongly dominated by holoplanktonic and meroplanktonic taxa which together comprise > 90 % of metazoans. Abundances of these taxa are not significantly different in the nocturnal samples but swimming harpacticoids increased by an order of magnitude (Table 1). Therefore, holo- and meroplanktonic taxa each comprised less than 30 % of the individu-

Table 1. Abundances $\cdot 10 \mathrm{dm}^{-3}$ of seawater ($\pm$ sd) and percentage composition of the metazoan fauna in diurnal and nocturnal plankton samples collected above an intertidal sandflat near the Island of Sylt (site III, August 27th and 28th, 1988). Copepod nauplii were excluded from this study. Minor taxa are not included in this table. *Arenicola marina* are all juveniles < 1 mm length. ** denotes a significant difference between daytime and nighttime samples (Wilcoxon matched pair signed rank test, $p < 0.01$)

Taxon	Daytime Abundance		%	Nighttime Abundance		%
Holoplankton, total	39.3	(18.1)	49	28.2	(13.7)	29
– Calanoidea	26.1	(11.4)		19.8	(12.1)	
– Rotatoria	5.9	(5.2)		2.9	(2.7)	
– Appendicularia	5.6	(4.4)		3.9	(2.2)	
– Chaetognatha	1.0	(0.9)		0.7	(0.7)	
– Plathelminthes	0.5	(1.0)		0.4	(0.7)	
Meroplankton, total	33.8	(26.9)	42	27.3	(9.6)	28
– Barnacle nauplii	17.9	(15.5)		9.2	(5.6)	
– Barnacle cypris	0.3	(0.5)		0.5	(0.7)	
– *Arenicola marina*	6.4	(5.9)		8.5	(7.3)	
– Spionid larvae	2.5	(2.2)		5.0	(3.6)	
– Nectochaeta larvae	4.1	(5.0)		3.2	(3.1)	
Semiplankton, total	4.8	(2.6)	6	40.4	(9.0)**	41
– Harpacticoids	4.5	(2.4)		39.5	(8.8)**	
– *H. flexus*	0.9	(0.9)		30.7	(5.8)**	
– Ectinosomatidae	0.3	(1.0)		5.3	(4.3)**	
Benthos, total	2.4	(3.0)	3	2.0	(1.1)	2
Total metazoans	80.3	(34.7)		97.7	(21.5)	

als in the nocturnal water column while harpacticoids were the most abundant taxon with the species *Harpacticus flexus* Brady & Robertson dominating. The percentage and abundance of suspended benthos (mainly Nematoda, Tardigrada and Ostracoda) are slightly higher in the daytime seawater samples, correlating with the higher waves. As *H. flexus* as well as some other species are very active swimmers which spend a substantial part of their life in the water column, they are henceforth denoted as "semiplankton" and thus separated from both entirely benthic species and species performing occasional migrations in the water column.

Low abundance of semiplankton during stormy nights

Increased current velocity during the stormy nights of September 11th and 12th was accompanied by an extraordinarily low abundance of semiplanktonic species in the water column. Compared to the daytime samples of September 8th, there was no significant increase in harpacticoid abundance during the stormy nights ($0.33 \pm 0.56 \cdot \mathrm{dm}^{-3}$ versus 0.51 ± 0.66 and $0.45 \pm 0.76 \cdot 1 \mathrm{dm}^{-3}$ of seawater, U-test: $p > 0.1$) while all other nighttime samples (n = 24 × 10 replicates) yielded significantly higher abundances of semiplankton than the respective daytime samples (see below).

No changes of semiplanktonic abundance with tidal height

Abundance of holoplankton and meroplankton in the water column above $100\,cm^2$ of sediment surface correlates positively with the height of the water column (r_s***; Fig. 2). In contrast, abundance of semiplankton per sediment surface unit remained fairly constant over the diel cycle but showed irregular variations at night (Fig. 2). Based on volume units of seawater, abundance of holo- and meroplankton remained fairly constant while the nocturnal abundance of both semiplankton and passively suspended benthos correlate negatively with tidal height (r_s***; Fig. 3). In the case of suspended benthos, the correlation is presumably caused by stronger wave erosion in shallow than in deep water. During the first 6 sampling dates, abundance of semiplankton shows a decrease which correlates significantly with increasing light during sunrise (r_s*).

Nocturnal dominance of semiplankton

In nocturnal shallow water, semiplankton can numerically dominate the zooplankton assemblage (Fig. 4). Semiplankton emerges from the sediment surface and the number of swimmers per surface unit remains rather constant over the tidal cycle. But increasing tidal height reduces their abundance per volume unit (r_s***). In contrast, holoplankton and meroplankton abundance per volume unit is rather constant, and increasing tidal height causes a higher abundance per surface unit (r_s***). On an average of the entire tidal cycles, semiplankton contributed 2.5 % of metazoan abundance in the water column during daytime, and 47.8 % at night (September and August samples, site II). In terms of biomass, the contribution is 2 % and 32 %, respectively. The metazoan biomass may thus be about 50 % higher at night. In the shallower water of site I, positioned higher up in the tidal gradient, the contribution of semiplankton to total mesozooplankton abundance may even exceed 60 % (Fig. 5).

Percentages of swimming harpacticoids

During daytime high tide of September 7th at site II, less than 1 % of the harpacticoids present in the superficial sediment layer swam in the overlying water column (Table 2). In the nighttime samples of August 8th at the same site, an average of 66 % of harpacticoids were simultaneously swimming in the water column. In the nighttime samples at site I (July 13th) as well as in some single sampling dates of August 8th (site II), the per surface area abundance of meiobenthic harpacticoids in the water column exceeded the abundance calculated from sediment sampling. This indicates a significant horizontal transport of harpacticoids with the tidal currents.

Specific composition of harpacticoids

During the entire period of investigation, the harpacticoid fauna of all sampled sites was strongly dominated by only two species, *Harpacticus flexus* and *Tachidius discipes* Giesbrecht. Together they comprised over 95 % of the harpacticoids, in the water column as well as in the upper (top 2 cm) sediment layer. Among the remaining species, *Longipedia helgolandica, Canuella perplexa, Intermedopsyllus intermedius, Mesochra*
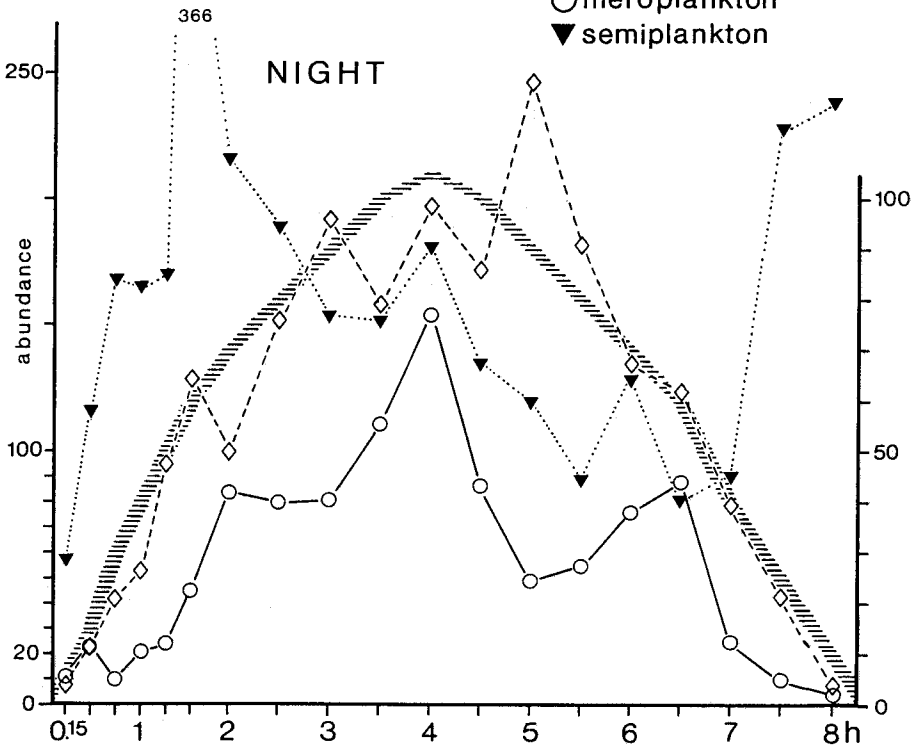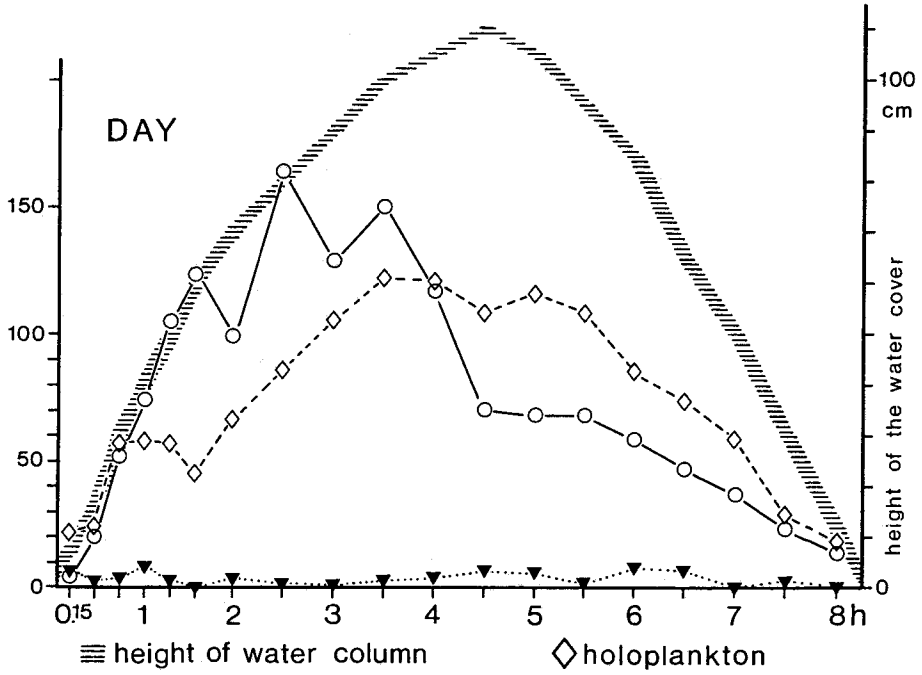
inconspicua, Evansula pygmaea, Paraleptastacus spinicauda and *P. holsaticus, Enhy-drosoma propinquum, Asellopsis hispida,* and *A. intermedia* could be identified (authorities of all species can be referred to in Mielke, 1975). Ectinosomatids and some copepodites remained unidentified. All species occurred both in the water column and in superficial sediment.

DISCUSSION

Specific composition of harpacticoid swimmers

The joint occurrence of all identified harpacticoid species in both the water column above and in the superficial sediment layer of the intertidal sandflats may in part be an artefact of (1) the stronger sampling effort in the water column (>500 samples of seawater but only 50 sediment samples), and (2) may result from passive suspension of some of the rarer species by wave action and tidal currents or sediment rafting (Hicks, 1988). In any case, the species list is subject to seasonal change. For instance, pilot sampling performed since April 1988 often revealed high abundance of the diosaccid *Amphiascoides debilis* (Giesbrecht) in both the sediment and the water column. At the same time, the dominants of July to September, *Harpacticus flexus* and *Tachidius discipes*, were significantly less abundant. These findings correspond to the annual abundance cycles of the latter two species in a nearby semi-exposed sandflat (Mielke, 1976). Their high abundance in the water column therefore may be restricted to the summer months. It is not known, up to now, if there are other species that take over their role in the water column during winter.

H. flexus and *T. discipes* are both widely distributed in the Wadden Sea and the adjoining brackish waters (Noodt, 1957). This wide distribution may relate to high tolerance to salinity and sediment type (especially in *T. discipes*, Noodt, 1957) and coincide with high nocturnal swimming activity. Up to 75 % of all *H. flexus* present in the sediment at low tide were simultaneously active in the water column during nocturnal high tide (Table 2). Therefore, the classification of this species as epibenthic seems no longer adequate, and a term such as semiplanktonic or semibenthic should be considered.

Tidal transport of semiplankton

In some cases, more harpacticoids were found in the water column than had been present in the sediment during the preceding low tide (Table 2). This demonstrates that high numbers of semiplanktonic species can be transported with the tidal currents and may explain some of the sudden changes of abundance in the sediment observed in previous studies (e.g. Palmer & Brandt, 1981; Willems et al., 1984). The significant increase in semiplanktonic abundance in the water column during nighttime when compared to daytime sampling with similar hydrographic conditions, and the lack of such

Fig. 2. Abundance of holoplankton, meroplankton, and semiplankton (left ordinate) in the water column over 100 cm² of sediment surface during a diel (Sept 7th) and a nocturnal (Aug 8th) high tide (site II). Abscissa indicates time (h) since sampling site was reached by the incoming tide
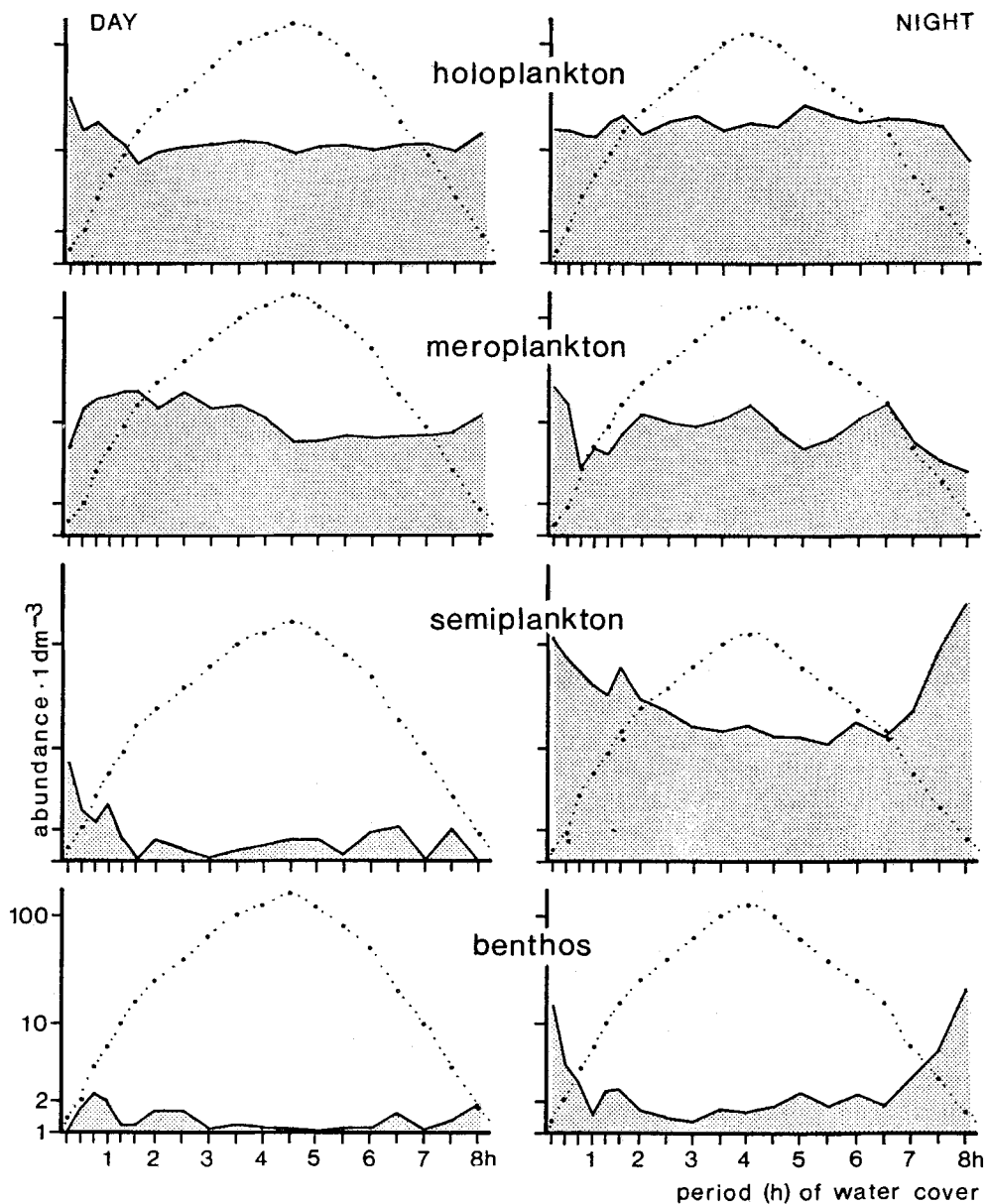
Fig. 3. Abundance [log(x + 1) transformed], per 1 dm³ of seawater, of holo-, mero- and semiplankton and suspended benthos above an intertidal sandflat (site II) during daytime high tide of September 7th and nocturnal high tide of August 8th. The dotted line indicates the height of the water cover
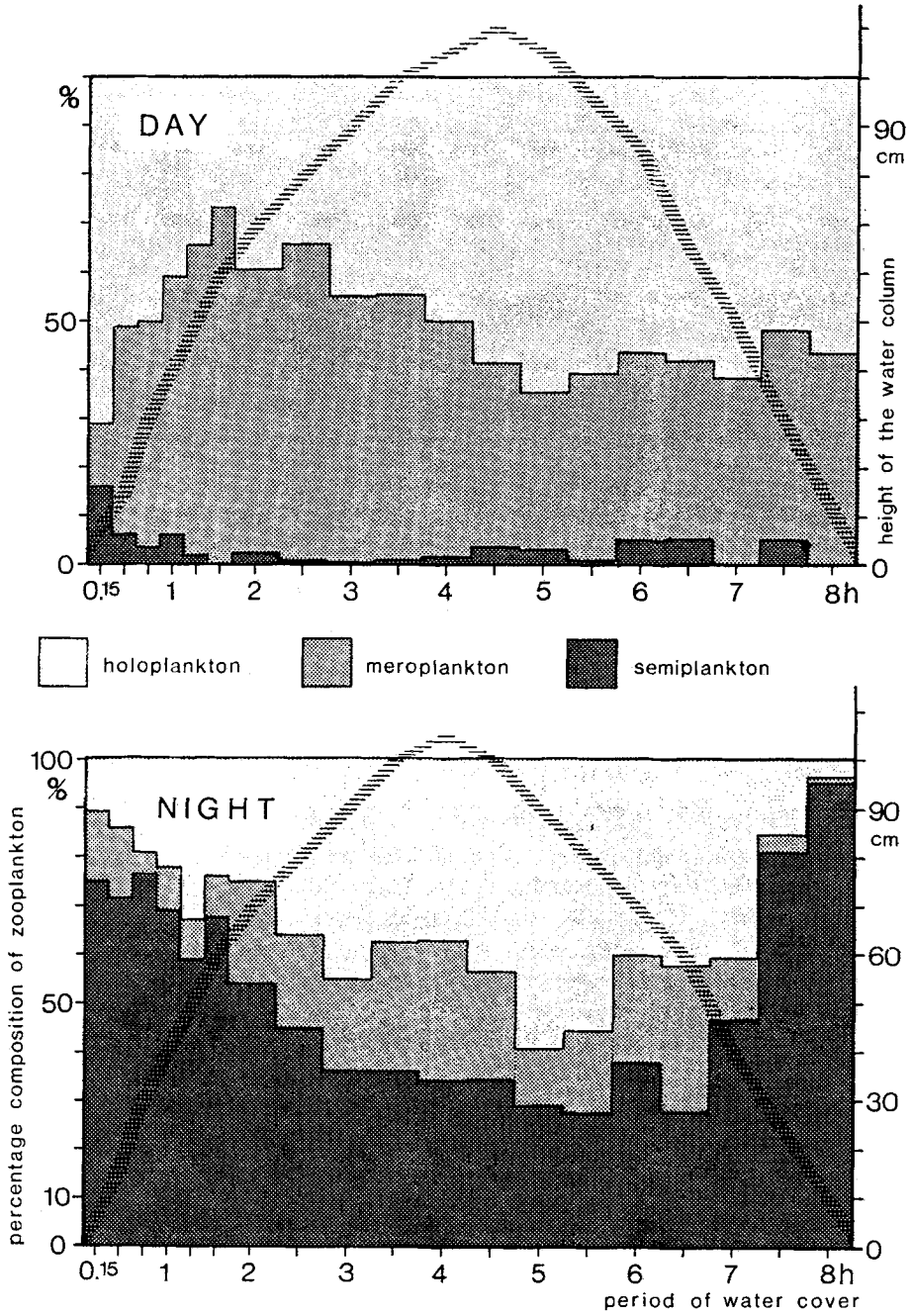
Fig. 4. Percentage composition of zooplankton in the water column above an intertidal sandflat (site II) during daytime high tide of September 7th and the nocturnal high tide of August 8th. The diffuse line marks the actual height of the water column (right scale)

Table 2. Average abundance of meiobenthic harpacticoids per m^2 of sediment surface area and in the overlying water column. In July site I, sediment samples were only once collected (during the intermittent low tide). At the other dates, sediment samples were collected during the low tide preceding the high tide of water sample collection

Site and Date	Taxon	Abundance in the	
		Water column	Sediment
(II) Sept. 7, daytime	Total harpacticoids	370	48,300
	H. flexus	305	31,700
(II) Aug. 8, nighttime	Total harpacticoids	15,730	23,700
	H. flexus	14,000	18,700
	T. discipes	1,320	4,200
(I) July 12, daytime	Total harpacticoids	2,030	4,200
(I) July 13, nighttime	Total harpacticoids	11,600	4,200

an increase during stormy nights both corroborate the thesis that emergence is primarily an active process in this intertidal assemblage. Contrasting results from other geographic areas (i.e. prevalence of passive suspension of organisms, e.g. Palmer, 1984; Palmer & Gust, 1985) may in part be explained by the non-linear response of harpacticoids to current speed (Armonies, 1988b). However, since emergence turned out to be a species-specific process (e.g. Walters, 1988) and most species have clear preferences for certain sediment properties correlating with the hydrographic conditions (e.g. Fenchel, 1978), variations in the degree of active swimming in the water column over sediment types are to be expected.

Semiplankton worldwide significant in shallow waters

The records of semiplanktonic species from other geographic areas (e.g. Hauspie & Polk, 1973; Porter & Porter, 1977; Hammer, 1981; Sibert, 1981; Fulton, 1984; Decho, 1986; Hicks, 1986; Jacoby & Greenwood, 1988; Walters, 1988) indicate that emergence of sediment-associated meiofauna may occur on a worldwide scale. However, the high increase of planktonic biomass by swimming meiofauna is certainly restricted to shallow inshore waters. Their abundance in the water column relates to units of sediment surface area and their abundance per volume unit decreases with increasing water depth. Therefore, their contribution to planktonic biomass will strongly decrease in deeper waters (Fig. 5). Thus, sediment-associated meiofauna is only an insignificant component of traditional ship-operated plankton samples (e.g. Hickel, 1975; Martens, 1980). However, semiplanktonic swimmers may aggregate close to the sediment surface, as has been demonstrated by D'Amours (1988). In deeper waters they might therefore play a role in the suprabenthos.

Semiplankton resembles macrofaunal suprabenthos

Meiofaunal emergence from the sediment resembles the life-style of suprabenthic amphipods and cumaceans. They also spend the daytime in superficial sediment layers and enter the water column at night (e.g. Hesthagen, 1973; Sainte-Marie & Brunel, 1985),
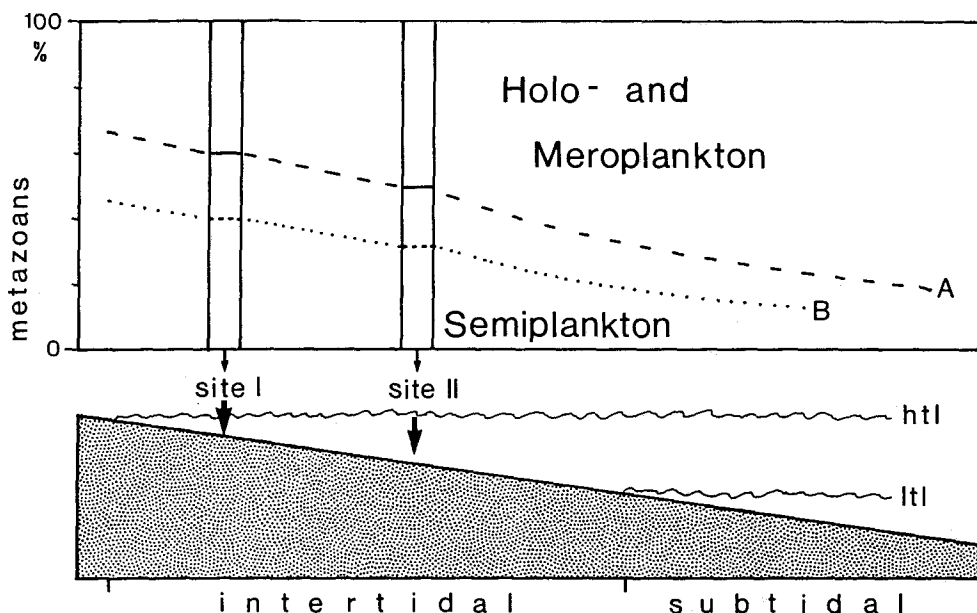
Fig. 5. Percentage composition of metazoans in the nocturnal water column at high tide above an intertidal sandflat (sites I, II) off the Island of Sylt, and the expected tendency along the tidal gradient. A: numerical abundance, B: biomass, htl, ltl: high and low tide level, respectively. For further explanations see text

although there were no significant dawn or dusk effects on swimming activity in the studied intertidal assemblage of harpacticoids (cf. Anger & Valentin, 1976). Possibly, these similarities in life-style reflect convergently evolved reactions to factors like endobenthic predation, effective in all size classes of benthic organisms.

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