Active emergence of meiofauna from intertidal sediment

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ABSTRACT: Laboratory experiments were conducted to test for active meiofaunal emergence from intertidal sediment in the absence of currents. Copepoda, Ostracoda, Plathelminthes and Polychaeta actively left submerged glass jars containing undisturbed sandy sediment. Ostracoda and juvenile Bivalvia moved to the sediment surface and climbed out of the glass jars while other taxa left the jars by swimming. In no case did Nematoda or Oligochaeta leave the sediment. During a single nocturnal high tide, 87 % of Copepoda, 67 % of Ostracoda and 42 % of Plathelminthes may leave the sediment. Emigration rates are significantly smaller during diurnal high tides. Copepoda were randomly distributed in the water column 10 to 50 cm above the bottom and Plathelminthes between 10 and 40 cm. There are specific differences in the emigration rates of plathelminth taxa. Diatom-feeders, copepod-feeders and unspecific predators emerged in significantly higher proportions than did nematode-feeders and bacteria-feeders. Results suggest high mobility and high transport rates of intertidal meiofauna above the sediment.

INTRODUCTION

Although meiobenthos was traditionally thought to be strictly infaunal, recent investigations report on meiofaunal occurrence in the water column (e. g. Alldredge & King 1977, 1980, 1985, Porter & Porter 1977, Hobson & Chess 1979, Hammer 1981, McWilliam et al. 1981, Sibert 1981, Ohlhorst 1982, Youngbluth 1982, Fancett & Kimmerer 1985, Hicks 1986, Walters & Bell 1986). Studies on recolonization of experimentally disturbed sediment and short-term meiobenthic surveys often yield indirect evidence for meiobenthos dispersing via the water column (e. g. Bell & Sherman 1980, Sherman & Coull 1980, Thistle 1980, Hockin & Ollason 1981, Palmer & Brandt 1981, Chandler & Fleeger 1983, Fleeger et al. 1984, Kern & Bell 1984). No regular emergence was found in the studies of Hagerman & Rieger (1981), Palmer (1984) and Palmer & Gust (1985), all of which were performed with muddy sediments. They concluded that the occurrence of meiobenthos in the water column is a passive process caused by erosion. In contrast most of the studies assuming active emigration of meiobenthos derived from sandy sediment or seagrass meadows. However, with the exception of Sibert (1981) and Hockin & Ollason (1981) all the above studies deal with tropical to warm-temperate

habitats, and direct evidence for meiobenthos entering the water column has up to now been restricted to subtidal areas.

In boreal intertidal and supratidal sand, meiobenthos performs more or less regular tidal vertical migrations in the sediment (Meineke & Westheide 1979). When the sand is disturbed by turbulence in the overlying water the majority of the fauna responds by downward migration (Boaden 1968); only various Copepoda and Plathelminthes move upward (Boaden & Platt 1971). Downward movement will reduce the risk of being suspended, and upward migrations will enhance suspension-rates. In muddy sediment, water flow causes only minor differences in the vertical pattern of meiofauna (Palmer & Molloy 1986) but above-ground structure (*Spartina* culms) may enhance copepod emergence under some hydrodynamical conditions (Palmer 1986).

The aim of this study was to investigate the rates of zoobenthos actively emerging from boreal intertidal sandy sediment. The passive component of meiobenthic occurrence in the water column was experimentally excluded – though not denied. Active emigration from the sediment may be a means of meiofaunal dispersal (Gerlach 1977, Alldredge & King 1980, Bell & Sherman 1980) but may also offer additional prey

(Decho 1986). On the other hand, meiofauna leaving the sediment may itself be subject to increased predation (Hobson & Chess 1976, Fulton 1982, Ohlhorst 1982). In many cases it is not known whether predators on meiofauna catch their prey in the water column, at the sediment surface, or by burrowing (e. g. Zander & Hartwig 1982, Sogard 1984).

MATERIAL AND METHODS

Sampling. For all experiments, samples were collected from a 30×30 m plot of the Königshafen wadden area near the Island of Sylt (North Sea). For a general description of the area see Reise (1985). The plot is rather sheltered and the sediment is mainly composed of medium sand (median diameter of sand grains 315 µm, sorting coefficient 1.5) with moderate amounts of detritus (loss on ignition 0.48 %). Experiments were performed between May and July 1987. Seawater temperature in May was 12 °C and increased to 15 to 16 °C in July. Air temperature varied between 10 and 20 °C. The sampled plot is positioned at mid-tide level (50 % tidal emersion); average tidal range is about 1.8 m in this area and about 0.9 m at the plot.

Sediment samples were collected with glass or plastic tubes to a depth of 2.5 cm. All experiments were simultaneously conducted in 10 aquaria (10 parallels). Samples were collected during low tide, about 2 h before the sample site was again flooded by the sea. These 2 h were used for transport to the laboratory and sample preparation. Thus the experimental submersion started at the same time as the sample site was flooded in the field.

Experimental treatments and null hypotheses. *Experiment I: Do meiobenthos actively leave the sediment?* Plastic aquaria (24 cm long and 12 cm wide) were filled with 2 l of filtered seawater and stored for 24 h to adapt to the experimental temperature of 12 °C ($=$ actual field temperature). Ten samples of 2 cm^2 surface area were collected at each of 5 sites and transferred into 10 cm^3 glass jars. In the laboratory, jars were cautiously filled with 12 °C filtered seawater without agitating the surface of the samples. Five samples (one from each site) were subsequently submerged into each of the 10 aquaria. For the next 4 d, benthos could emigrate from the sediment and swim or climb into the aquaria. To record the course of emigration, the jars were transferred to a second set of aquaria after fixed periods and the water of the previously used aquaria poured through 63 µm meshes to retain emigrated fauna.

With modification of the light regime, the experiment was repeated 3 times: Expt Ia was performed in con-

tinuous light (50 µE m^{-2} s^{-1}) with water exchange every 24 h. Expt Ib was performed in continuous darkness except when transferring the glass jars into a new set of aquaria which was done every 24 h. Finally, Expt Ic was performed under a 18/6 h day/night rhythm with water exchange every 6 h.

Expt I tested the following hypotheses:

H_o (1): There is no active emigration of benthos from the sediment – faunal abundance in the experimental aquaria does not significantly differ from zero.

H_o (2): Emigration is random in time – the rates of emigrating fauna do not differ among the 4 d of experimentation.

H_o (3): There are no differences in the percentage emigration rates between taxa – all taxa behave the same.

Experiment II: Percentage emigration during one tidal cycle of submersion. Experimental design was as Expt I, with 2 exceptions: (1) smaller aquaria were used (400 cm^3 seawater instead of 2000 cm^3) and only one glass jar with sediment was submerged per aquarium; (2) glass jars containing the sediment were transferred to a new set of aquaria at 1 h intervals (total 6 h). The size of sediment samples was 1 cm^2 surface area, sampled to a sediment depth of 2.5 cm. Expt II was performed twice: Expt IIa during daytime, with light (50 µE m^{-2} s^{-1}), and Expt IIb during night-time, in the dark. It tested the hypothesis

H_o (4): The pattern of emergence is random over time (6 h).

Experiment III: Distance meiobenthos swims above bottom. The previous experiments monitored the rate of benthos leaving the sediment, either swimming or climbing out of the jars. Expt III only recorded actively swimming benthos and tested the hypothesis H_o (5)· There is no difference in the abundance of swimming benthos between 10 and 50 cm above bottom.

Ten plastic barrels (34 cm in diameter and 57 cm high) were filled with filtered seawater to a height of 55 cm. As a source of swimming benthos, 3 Petri dishes containing 60 cm$^2 \times 1$ cm surface sediment were submerged into each of the barrels. These dishes were initially filled with filtered seawater to the rim, any material adhering to the water surface was removed by slight decantation, the dishes were again filled with seawater and finally cautiously submerged into the barrels. Five plastic boxes of 500 cm^3 volume were submerged into each barrel without contact to the ground or side walls. There was no possibility of entering the boxes other than by swimming. The upper rim of the boxes were 10, 20, 30, 40, and 50 cm above ground, respectively. Boxes were removed after 6 h storage in the dark and their water content sieved through 63 µm meshes to retain swimming benthos.

***Experiment IV: Specific composition of emigrating
and non-emigrating Plathelminthes.*** Fewer species
were recorded as active emigrators in the previous
experiments than are normally found in the sampled
tidal flat. Expt IV checked for specific differences in the
plathelminth emergence pattern. It tests the hypothesis
H_o (6): There is no difference in the rates of emigration
between plathelminth species (subordinated taxa,
feeding types).

No extra experiments were performed to check for
this point. Instead, the species composition of Plathel-
minthes emerging in Expt Ib was compared to the
species composition of non-emigrators.

Test of experimental methods. Sediment sampling
causes at least slight mechanical disturbance of the
sediment structure. Meiofaunal behavior might be
influenced by these disturbances, resulting in artifacts
in the experiments outlined above. The effect of
mechanical disturbance on meiofaunal emigration was
tested using experimental designs like Expt II on
6 levels of mechanical disturbance:
(1) Sampling tubes were closed at the bottom and
directly used in experiments – no transference into
glass tubes.
(2) 'Normal sampling': cores were sampled with plas-
tic tubes and transferred into glass tubes for transport
and experimentation – slight deformation of the sedi-
ment structure.
(3) 'Normal sampling' + mechanical stirring of the
sediment.
(4) 'Normal sampling' + destruction of the sediment
structure by shaking of the glass containers.
(5) 'Normal sampling', but the sediment column was
turned upside down.
(6) Combination of (3) and (4) to completely destroy
the sediment structure.

With the exception of Plathelminthes which left the
sediment turned upside down at significantly higher
rates(U-test, $p < 0.001$) when compared to (1) and (2),
the above treatments did not affect emigration rates in
the previously described experimental design. How-
ever, this does not mean that meiobenthos might not
generally be susceptible to this kind of disturbance. To
avoid inadmissible generalization beyond the level of
this study, I will not present any further data. They can
be obtained on request.

Statistical treatment. In general, abundance data
differ significantly from a normal distribution. There-
fore, the non-parametrical U-test (Wilcoxon et al., in
Sachs 1984) is used throughout as a conservative mea-
sure. Significant results are indicated by $^*(p < 0.05)$,
$^{**}(p < 0.01)$ and $^{***}(p < 0.001)$. The standard deviation
given in the tables does not intend to describe the data
distribution but is used to indicate the range of varia-
bility.

RESULTS

Taxonomic composition of the metazoan benthos at the sampled plot

Ten sediment samples of $2 \, cm^2$ surface area (0 to
2.5 cm layer) were randomly collected at the sample
site (20 June 1987). Grain-by-grain sorting of these
samples (without fixation) yielded an average of 1906
metazoans below $10 \, cm^2$ surface area. Nematoda were
most abundant (990 ind. $10cm^{-2}$ = 51.8 % of metazoan
benthos), followed by Copepoda (520 ind. $10cm^{-2}$ =
27.2 %), Ostracoda (198 ind. $10cm^{-2}$ = 10.4 %),
Polychaeta (4.1 %), Oligochaeta (3.5 %), and Plathel-
minthes (2.7 %). Other taxa, such as Gastrotricha,
Gnathostomulida and Halacarida were present but
together supplied < 1 % of metazoans.

Experiment I: Do meiobenthos actively leave the sediment?

Copepoda, Ostracoda and Plathelminthes left the
sediment in significant numbers in all 3 trials of Expt I.
The number of emigrating Polychaeta was significantly
different from zero only in the continuously dark and
the day/night-rhythm trials. No significant emigration
was found in Nematoda and Oligochaeta in either case,
although they are major components of the benthos at
the sampled site. Veliger-larvae of *Littorina littorea* L.
and juvenile Bivalvia (mainly *Cerstoderma edule* [L.])
also emigrated from the sediment. Veliger-larvae
behaved similarly to Copepoda and juvenile Bivalvia
behaved like Ostracoda. Both groups are however not
mentioned further.

Sorting of the sediment after 4 d of submersion was
performed on all 50 samples of Expts Ib and on 10
randomly chosen samples of Expts Ia and Ic. The
corresponding numbers of animals that remained in the
sediment allow for an estimate of the percentage of
emigrated specimens (Table 1). Though the 3 trials
were not simultaneously performed and are thus not
adequate to test for the influence of light, the percent-
ages indicate higher activity during darkness. This is
also seen in the periodical increase of emigrating
benthos in Expt Ic (Fig. 1). Significantly more speci-
mens emigrated in the dark period than in the light.
However, such a pattern might also be caused by an
endogenous diurnal rhythm.

Since the number of emigrating benthos seems to be
increased by continuous darkness and decreased by
continuous light, Expt Ic with an 18/6 h day/night
rhythm is most appropriate to judge on the mobility of
benthos (Table 1). The percentage of Copepoda leav-
ing the sediment during the first days, however, is too

Table 1. Abundance of emigrated fauna in Expts Ia (l, light), Ib (d, darkness) and Ic (l/d, light/darkness), and average number of specimens that remained in the sediment. Total: sum of emigrated fauna (within 96 h) and fauna that remained in the sediment. $\bar{x}$: mean; SD: standard deviation; %: percentage of totals

| Taxon | | Emigrated | | | | | | Total | Remained in sediment |
| | | Within 24 h | | | Within 96 h | | | | |
		$\bar{x}$	SD	%	$\bar{x}$	SD	%	$\bar{x}$	$\bar{x}$
Copepoda	l	19.8	4.0	11.8	57.5	11.6	34.4	167.3	109.8
	d	305.5	58.6	95.9	318.1	65.8	99.8	318.7	0.6
	l/d	601.9	95.4	46.1	1200.7	152.4	92.0	1305.3	104.6
Ostracoda	l	3.2	2.4	3.1	10.0	3.4	9.6	104.0	94.0
	d	125.1	30.1	65.4	169.1	40.4	88.4	191.2	22.1
	l/d	116.0	17.9	58.8	177.6	32.2	90.0	197.2	19.6
Plathelminthes	l	5.1	2.4	3.0	17.7	5.7	10.4	169.8	152.1
	d	7.2	4.5	34.8	12.3	5.0	59.4	20.7	8.4
	l/d	3.5	1.8	7.2	16.2	4.9	33.3	48.6	32.4
Polychaeta	l	0.2	0.3	0.2	0.4	0.7	0.4	92.9	92.5
	d	1.9	1.9	3.1	8.7	4.3	14.1	61.9	53.2
	l/d	0.6	0.7	1.0	2.2	1.8	3.4	63.9	61.7
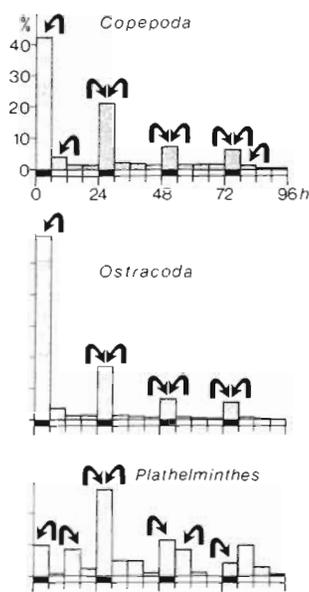
Fig. 1. Course of emigration during 4 d of submergence (Expt Ic, 18/6 h light/dark cycle). Percentages of the totally emigrated number of individuals per taxon. Arrows indicate a significant difference between succeeding periods (U-test, $p < 0.05$). Decrease in numbers over time results from the emptying of sediment cores through emigration. Black and white fields below columns indicate darkness and light, respectively

small because of high numbers of nauplius-larvae (not included) and copepodites (included in copepods) in the sediment. Development of nauplius-larvae to copepodites increased the emigration rates of the final days and the totals.

Since Nematoda and Oligochaeta remained in the sediment while other taxa at least partly emigrated, the

taxonomic composition of emigrated fauna is different from that of fauna remaining in the sediment (significant differences in the rank order of abundance; Fig. 2).

From Expt I, the following conclusions can be derived:

(1) For the taxa Copepoda, Ostracoda, Plathelminthes and Polychaeta, H_0 (1) is rejected. Members of these taxa actively emigrated from the sediment.

(2) In the case of Copepoda, Ostracoda and Plathelminthes, emigration shows a marked periodicity coinciding with and possibly caused by differences in the light regime. H_0 (2) should therefore be rejected. However, based on the number of animals that stayed in the sediment up to a distinct point in time, the percentages of Ostracoda and Copepoda leaving the sediment per day do not significantly differ. In retrospect it seems a fairly constant percentage of copepods left the sediment per day, causing a continuous decrease in numbers. With regard to the percentage emigration, H_0 (2), hypothesising no differences in emigration among the 4 d, is accepted.

(3) H_0 (3) is rejected. The percentage taxonomic composition in the sediment significantly differs from that of the emigrated fauna.

Experiment II: Percentage emigration during one tidal cycle of submersion

Altogether 87 % of Copepoda, 67 % of Ostracoda, and 42 % of Plathelminthes left the sediment during a single simulated nocturnal high tide. The respective percentages were considerably smaller during a diurnal high tide (Fig. 3). All percentages should be regarded as minimum values: possibly some specimens

Fig. 2. Changes in the rank order of taxa between the fauna of original sediment (not submerged but sorted immediately), emigrated fauna, and the fauna remaining in the sediment after 4 d of submersion (Expt Ib). Ranks are based on significant differences in abundance (U-test)
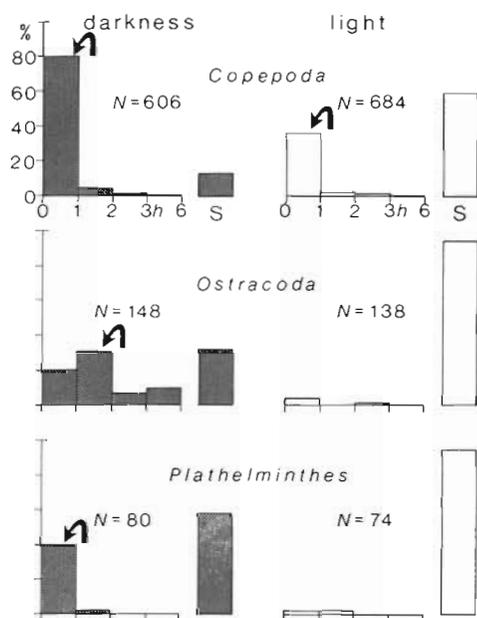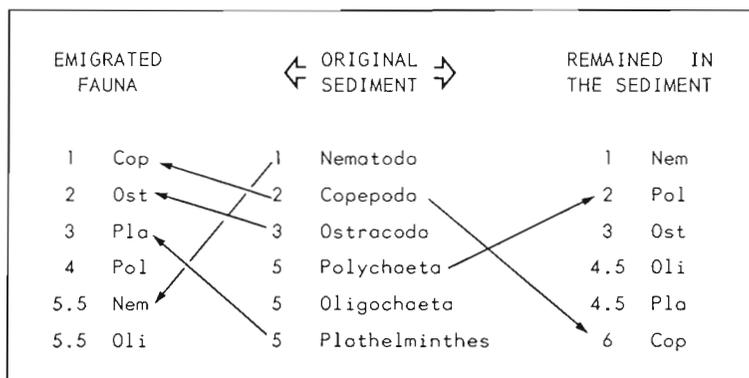
Fig. 3. Course of emigration during 6 h of submersion (Expt II). Percentages of total abundance (N; ind. $10 \mathrm{cm}^{-2}$). S: percentage remaining in the sediment. Because of low abundance the period 3 to 6 h is combined. Arrows indicate significant difference between successive periods

emerged from the sediment but returned prior to sampling. Calculating from the base areas of the glass jars (2.5 cm^2) and aquaria (50 cm^2), the probability of a swimming animal returning accidentally to the inner glass jars with sediment is about 5 %. Since the natural sediment might be more attractive than a bare plastic ground, the degree of underestimation may even be higher than 5 %.

Copepoda and Plathelminthes show maximum emigration rates during the first hour of submersion (Fig. 3). Ostracods need more time to climb out of the glass jars. This might either indicate a true delay in their activity, or might be an artifact of the unnatural glass container. However, in all cases considerable numbers of animals emerge during 1 h of submergence without

currents. During slack tides, there are periods of similar length without strong currents in the field, and corresponding emergence of these taxa is expected. H$_o$ (4), hypothesising a random pattern of emigration over 6 h, is rejected.

Experiment III: Distance meiobenthos swims above the bottom

Although Ostracoda were highly active under comparable conditions in Expts I and II they were only once found in a submerged box. There is no hint that Ostracoda are able to swim actively. Among the active swimmers, only Copepoda and Plathelminthes were in sufficient numbers for a statistical evaluation. Abundance of Copepoda did not significantly differ between the boxes fixed between 10 and 50 cm above ground (Fig. 4). In the case of Plathelminthes the uppermost box contained fewer individuals, which is significant on a 5 % level, but not significant when p is adjusted to an adequate level for 10-fold multiple comparisons. There was no difference between the other heights. Thus, concerning Copepoda and Plathelminthes, H$_o$ (5) is maintained.

Experiment IV: Specific composition of emigrating and non-emigrating Plathelminthes and Polychaeta

In Expt Ib, sediment samples were submerged and significant numbers of Plathelminthes swam out into the water column. After 4 d, all samples were sorted for the benthos that remained in the sediment. Comparing the numbers of emigrators versus non-emigrators, significant differences appear between taxa as well as trophic groups (Table 2). Significantly more Proseriata, Typhloplanoida and Dalyellioida emerged from the sediment while more Kalyptorhynchia rested in the sediment. On the species level, *Promesostoma meixneri* Ax, 1951, *Pogaina suecica* (Luther, 1948), *Provor-*
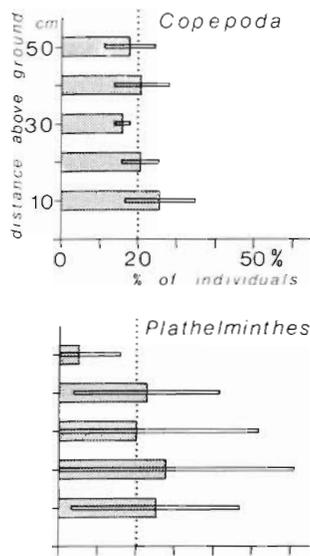
Fig. 4. Distribution of Copepoda and Plathelminthes over boxes submerged in barrels (percentages per height, standard deviation; Expt III). Dotted line: 20 % level expected in the case of completely regular distribution over the entire range

tex tubiferus Luther, 1948, Provortex psammophilus Ax, 1951 and Cheliplanilla caudata Meixner, 1938 all emigrated in significant numbers. Bresslauilla relicta Reisinger, 1929 and Neoschizorhynchus parvorostro Ax & Heller, 1970 on the other hand, preferred to remain in the sediment during the 4 d of submersion.

Much of this variability is explained by the type of feeding (Table 2). The majority of copepods emigrated

from the sediment, and copepod-feeding Plathelminthes did the same. Correspondingly, no nematode emigration was observed, and most of the nematode-feeding Plathelminthes stayed in the sediment just as did bacteria-feeders. Diatom-feeders and unspecific predators on meiofauna and microfauna preferred to leave the sediment.

Because of low abundance, no significant correlations were found between polychaete emergence and their feeding-types. However, there were specific differences in the emigration rates. Juvenile (mostly < 1 cm long) Nereis diversicolor O. F. Müller emigrated in the highest percentage, followed by Eteone longa (Fabricius). Anaitides mucosa (Oersted) and Pygospio elegans Claparède were already scarce and others, such as Scoloplos armiger (O. F. Müller), which is the dominant polychaete at the investigated site, were never found in the water column.

DISCUSSION

Behavioral versus physically forced emergence

This study revealed 2 causal factors urging benthos to enter the water column: (1) Most of the emerged harpacticoids and Plathelminthes left the sediment immediately after submersion. Significant differences in the course of emigration indicate that emergence is not just a casual event in these taxa but seems to be regular, possibly triggered by endogenous factors. (2)

Table 2. Plathelminth taxa that showed significant differences between abundance in water column (emigrators) and in sediment (non-emigrators) after 4 d of submersion in the dark (Expt Ib). x: Average abundance per 10 cm^2 of sediment surface; SD: standard deviation; *, **, *** Significance level (U-test, $p < 0.05$, 0.01, 0.001 respectively). Non-significant comparisons are omitted. B, C, D, N, P: feeding types (see below)

Taxon and feeding types	Emigrators		Non-emigrators	
	x	SD	x	SD
Proseriata (P)	1.3	1.42**	0	
Typhloplanoida (mostly C)	1.7	1.16**	0.3	0.48
Promesostoma meixneri (C)	1.1	1.37**	0	
Kalyptorhynchia (B and N)	0.5	0.53	3.7	2.31**
Cheliplanilla caudata (N)	0.5	0.53*	0	
Neoschizorhynchus parvorostro (B)	0		1.8	1.32***
Dalyellioida (D, B and P)	7.9	3.78*	4.2	2.53
Pogaina suecica (D)	4.0	3.13***	0.3	0.67
Bresslauilla relicta (B)	0.2	0.42	1.9	1.45**
Provortex tubiferus (D)	1.6	1.35***	0	
Provortex psammophilus (P)	0.8	0.63**	0.1	0.32
Feeding types:				
D Diatom-feeders	7.6	3.86**	2.4	1.43
B Bacteria-feeders	0.2	0.42	3.7	2.54***
C Copepod-feeders	1.5	1.35*	0.2	0.42
N Nematode-feeders	0.5	0.53	1.7	1.34*
P Unspecific predators	2.2	1.55***	0.1	0.32

In the polychaete *Pygospio elegans* emigration occurred only after 1 d of submersion and was possibly caused by deterioration of environmental factors. This might also be the cause for the significantly higher number of Plathelminthes that left the glass jars after the sediment had been turned upside down. Further deterioration of physical factors such as oxygen content in experiments longer than 4 d might lead to emergence of additional taxa (cf. Lorenzen et al. 1987).

The rapid emigration during the first 1 to 2 h of experimental submersion in Copepoda, Plathelminthes and Ostracoda indicates that deterioration of physical factors is not the cause for their emergence – or else the physical factors had already been extremely unfavourable in the field. However, as indicated by the effect of light (Fig. 1), physical factors such as the light regime, oxygen availability, and salinity do influence emigration rates (Armonies unpubl.), and biotic factors might similarly be involved.

The 'laboratory environment' may be another factor influencing emigration rates. Although the effects of mechanical destruction of the sediment structure do not indicate that the sampling procedure was harmful, there is so far no adequate test for other factors.

All of the experiments described above were performed in the absence of flow. However, flow as well as other hydrodynamic factors like hydrostatic pressure may strongly influence the behavior of meiobenthos (e. g. Boaden 1968, Fegley 1987). Therefore further experiments were conducted to test for differences in the emigrative behavior in gradients of physical factors such as temperature, salinity and flow (Armonies unpubl.). Results indicate that emergence is not an artifact of the no-flow conditions, although the emergence pattern is indeed influenced by flow.

As a result of varying degrees of environmental harshness and specific differences in the tendency to leave the sediment, a regular gradient is expected between plankton occasionally touching the sediment and benthos occasionally emerging from the sediment. On such a scale, Nematoda are relatively benthic and most Copepoda are relatively planktonic. However, this classification only meets the situation in the studied intertidal sand flat. On more exposed beaches epibenthic harpacticoids become rare (Mielke pers. comm.), and interstitial species might be more benthic. The fauna of muddy sites, on the other hand, seems to include some good as well as bad swimmers (Palmer 1984).

In Plathelminthes and Polychaeta it seems that the emergence rates can roughly be estimated by the swimming ability of the respective species (observation of the swimming ability in Petri dishes after mechanical stimulation). Some differences also exist in copepods: the slender interstitial species tend to emigrate less rapidly than do the more voluminous epibenthic harpacticoids. Bell et al. (1987) reported on significant correlations between morphological indices and the habitat utilization and type of movement in seagrass harpacticoids.

Consequences of emigration on distributional patterns

As a consequence of active emigration from the sediment, short-term temporal variations in abundance and population structure are expected, and for harpacticoids have already been demonstrated by Kern & Bell (1984). Specific differences in the tendency to leave the sediment (as demonstrated in Polychaeta and Plathelminthes) may also cause short-term changes in the faunal composition. Tischler (1979, p. 125) proposed differentiating any list of species obtained from a single habitat according to categories such as 'indigenous species', 'visitors', and 'guests'. In the light of high meiobenthic mobility, this suggestion seems also to be appropriate for meiobenthic organisms, especially in community studies and environmental monitoring.

Potential benefits versus potential risk of emersion

In Expt II (6 h submersion in the dark) an average of 48 copepods emigrated per 1 cm^2 of sediment surface during the first hour of submersion (Fig. 2). Since the period of swimming activity of a single specimen is not known, the actual abundance of benthos in the water column can only be estimated: provided a single specimen swims no longer than 5 min, up to 40 000 copepods m^{-2} are simultaneously active in the water column. Likewise, if the swimming period is only 1 min 8000 harpacticoids above 1 m^2 of sediment surface should be attractive enough to be a remunerative source of food, e. g. for juvenile fish (Alheit & Scheibel 1982, Pihl & Rosenberg 1984, Pihl 1985). Small size-classes of the goby *Pomatoschistus minutus* (Pallas) even seem to prefer benthic harpacticoids to planktonic calanoids (Zander & Hagemann 1987). Possibly the benthic harpacticoids are easier to catch than calanoids. The higher nocturnal than diurnal swimming activity may be useful in avoiding visual predators (Hobson & Chess 1976, Greening & Livingston 1982, Ohlhorst 1982, Fancett & Kimmerer 1985) and the joint emergence of many specimens during a restricted period may be another way to reduce each individual's risk of being preyed upon.

Additional prey (Decho 1986) and the possibility of dispersal are advantages of emergence. Species with a high rate of emersion might additionally increase their

abundances from a small-scale towards a larger-scale carrying capacity and thus more intensively exploit resources (see Thistle 1980). Possibly emergence can also help to escape predation within the sediment. The high rates of emergence, despite the risk of being preyed upon, indicate alone that there must be a net advantage in regularly leaving the sediment, or, at least, no disadvantage.

Emergence increases the stability of the benthic system

From an ecosystem point of view, emergence from the sediment is regarded as an efficient way of energy exchange between the benthos and pelagial. A high abundance of food items in the water column can be transferred to the benthos even before being sedimented and an exceptionally high abundance of swimming benthos will presumably increase the rate of predation by pelagic predators. Small-scale disturbances of the benthic system may likewise be rapidly compensated for (e. g. Sherman & Coull 1980, Thistle 1980, Hockin & Ollason 1981, Palmer & Brandt 1981, Chandler & Fleeger 1983). Thus, high mobility may increase the persistence of the benthic system and its ability to absorb changes and disturbance and still maintain the same relationships between species or state variables (= resilience; Holling 1973).

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