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ARMONIES

Assemblage of Free-living Plathelminthes on an Intertidal Mud Flat in the North Sea

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Contents

Abstract

A quantitative survey of the Plathelminthes living in soft mud in the intertidal zone of Königshafen (isle of Sylt, North Sea) was conducted from November 1982 to June 1983. Abundance was highly variable but high on the average (260 Individuals 10 · cm^{-2}). The number of species (49) and diversity was lower compared to adjacent sand flats. Most individuals (81 %) feed on diatoms, and average body size is small (90 % were < 1 mm in length).

Pogaina suecica was abundant throughout the study period, while other species fluctuated strongly. *Microstomum papillosum* showed a mass development in February and *M. bioculatum* in May. Both species reproduce by paratomy. The rapidly reproducing Acoela *Archaphanostoma agile* and *Philactinoposthia saliens* were other abundant diatom-feeders. Abundant predators were *Proxenetes quinquespinosus, P. quadrispinosus* and *Promesostoma gracilis.* It is suggested that the high variability in the plathelminth assemblage of the mud flat is caused by fluctuations in the major food source (diatoms), and by the lack of refuges below the mud surface.

A. Introduction

Free-living Plathelminthes are a predictable and important component of the meiofauna dwelling in coastal marine sands and comprise usually between 5 and 10 % of total abundance (Ax and Ax 1970, Boaden and Platt 1971, Gray and Rieger 1971, Reise 1984, Schmidt 1968). In coastal mud flats, meiofauna occurs with about twice the abundance than in equivalent sandy sediments (Coull and Bell 1979), however, Plathelminthes are hardly ever mentioned in general studies on meiofauna in mud (i. e., Coull and Wells 1981, Dye 1983, Rees 1940, Warwick et al 1979), except by Bouwman et al (1984), Ellison (1984) and Montagna et al (1983). Suspecting that this apparent scarcity of Plathelminthes in coastal mud is due to sampling technique, we conducted a quantitative study on an intertidal mud flat, adjacent to sandy areas which have been investigated previously (Reise 1984, Schmidt 1968, Xylander and Reise 1984).

Plathelminthes comprised between 9 and 15 % of total meiofauna in the mud, and diatom-feeding species dominated over carnivors. Compared to sandy flats, abundance is relatively high while diversity is low.

B. Material and Methods

1. Sampling and Processing of Samples

Sediment samples in the mud were taken with a plastic corer of 2.2 cm inner diameter. Mud was sucked in by using a piston. Samples were taken to a depth of 1.5 cm. Preliminary investigations showed that 96.4 % of the Plathelminthes live in the upper 1 cm of this mud.

Sampling occured at low tide. Two sites of 0.3 m^2 were selected. One was positioned on a mud bank, emerging at low tide, the other in a mud depression covered by residual water throughout low tide period. The two plots were approximately 20 m apart and 20 samples were taken from each, in November 1982, February and May 1983. Additional samples were taken in the course of a spatial analysis all over the muddy area of 0.5 km^2, from mats of macroalgae, and in the overlying water.

Plathelminthes are difficult to extract from muddy substrates, because mud particles resemble the Plathelminthes both in size and in specific gravity. ARMONIES and HELLWIG (in prep.) invented a method where Plathelminthes migrate along an oxygen gradient from mud into sand. They are separated from the sand by repeated shaking and decanting. The detailed procedure was as follows:

(1) Mud samples are covered with a 2.5 cm layer of cleaned sand (particle size 0.7 to 1.0 mm) and saturated with sea water.
(2) Storage in the dark at 3 to 4 °C below field temperature for at least 24 h.
(3) Transfer of the sand fraction into a beaker and decantation through a set of sieves with 125, 80 and 40 µm mesh size. Decantation is repeated several times with added sea water and increased shaking intensity.
(4) Sand fraction is replaced back to its original mud sample.
(5) Storage in the dark at room temperature for at least one day.
(6) Second processing as described in (3).

All samples were processed within two weeks. Each sieve fraction was washed into a petridish of 8 cm in diameter and the Plathelminthes were counted and measured under a stereo microscope (8 × and 24 ×), and identified to species level at higher microscopic magnification. Samples were neither narcotized nor stained.

With this method we obtained more than 80 % of the Plathelminthes and no significant difference was found compared to direct counts from samples washed into several petridishes without sieving. The latter procedure, however, was more time consuming.

2. Study Area

Investigations were carried out in Königshafen, a sheltered marine bay near the isle of Sylt in the North Sea (Fig. 1). Ecological characteristics of the area are given in WOHLENBERG (1937) and REISE (1978). We investigated a mud flat of 0.5 km^2 in the inner part of Königshafen, a muddy depression which in its central part remains submerged even during low tide. Physical conditions and sediment qualities are given in Table 1. Tides are semidiurnal. The duration of emergence varied according to moon phase, wind force and direction, and lasts

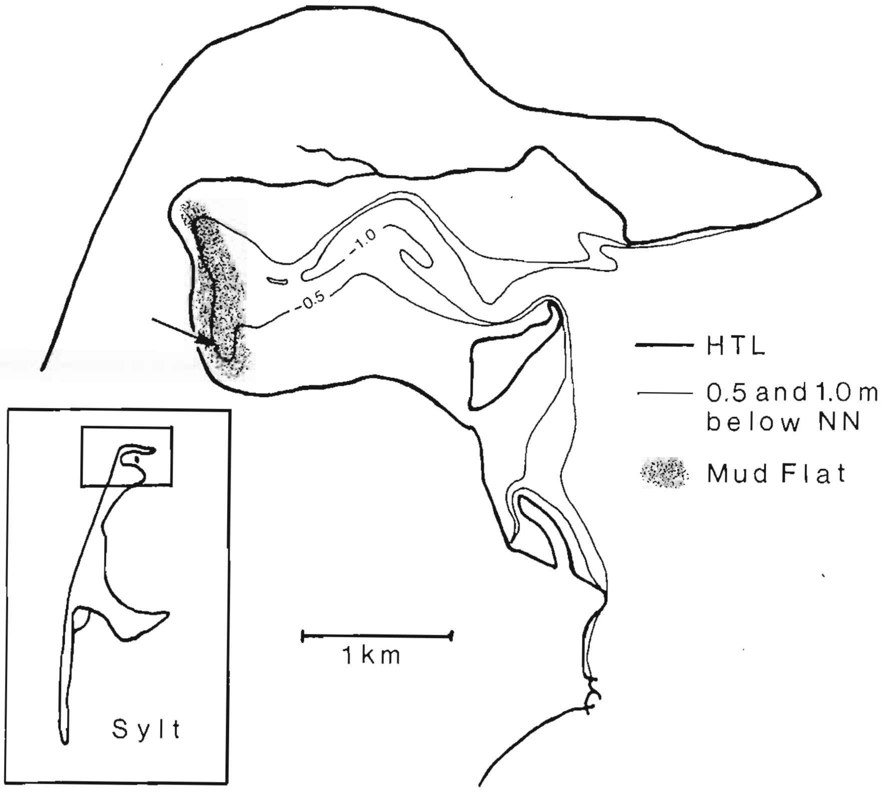

Fig. 1. Northern part of the isle of Sylt with intertidal area of Königshafen. HTL = high tide line; −1.0 m corresponds approximately to spring low tide line; arrow points to sampling site.

from total submergence to 8 h of exposure. Sediment temperature almost equaled water temperature and was about two degrees warmer than the air (measured at low tide throughout the spring).

Particle size of the mud was determined by wet sieving through a set of sieves with 500, 250, 80 and 40 µm. Weight of fractions as well as the residue (< 40 µm) was determined after drying for 40 h at 95° C. Median particle diameter and the amount of the silt fraction (< 63 µm, 82 %) were derived from cumulative data plotting. Ignition loss at 550° C (5 h) was taken as a measure of organic content. Chlorides had been removed previously by repeated washing with freshwater. Recent analyses by Dankers and Laane (1983) showed that data for organic content yielded with this method are four times too high. A difference was found in organic content between tidal (9.3 %) and permanently submerged parts (7 %) of the mud flat.

Table 1: Habitat characteristics of the mud flat in Königshafen, isle of Sylt.

Depth at high tide (cm)	80
Average duration of exposure (h)	4
Salinity (‰)	28–32
Median grain size (µm)	40
Water content of sediment at low tide (%)	70
Organic content	
(ignition loss in % of dry weight)	9.3
Diatoms (cells · 1 cm^{-2} in December 1982)	46 000
Meiofauna (individuals · 10 cm^{-2})	
December 1982	2 010
June 1983	2 173

Brownish sediment extends to a depth of 10 mm. It is very flaky and partly converted into faecel pellets by grazing molluscs. Below this layer the mud is black.

C. Results

1. Species Composition

We encountered a total of 49 plathelminth species dwelling in the mud of Königshafen (Table 2). Most of the species belong to the Rhabdocoela (Typhloplanoida, Kalyptorhynchia, Dalyellioida). The Acoela and Macrostomida do not comprise many species but occur in high numbers of individuals. Most genera are only represented by one or two species. Exceptions are the thyphloplanoid genera *Promesostoma* and *Proxenetes*, each with six very similar species

Table 2: Plathelminth species recorded on a mud flat in the inner part of Königshafen, isle of Sylt, from October 1982 to June 1983. The total number of individuals found is given, and the feeding type is indicated as p = predator, g = grazer and m = mixed feeder. Only adult species are listed.

Acoela		
Pseudaphanostoma brevicaudatum Dörjes, 1968	352	g
Pseudaphanostoma pelophilum Dörjes, 1968	142	g
Pseudaphanostoma psammophilum Dörjes, 1968	3	
Archaphanostoma agile (Jensen, 1878)	2011	m
Praephanostoma chaetocaudatum Dörjes, 1968	3	
Anaperus tvaerminnensis (Luther, 1912)	1	p
Philachoerus johanni Dörjes, 1968	54	p
Philactinoposthia saliens (Graff, 1882)	777	m
Mecynostomum auritum (Schultze, 1851)	181	m

Macrostomida		
Macrostomum pusillum Ax, 1951	40	g
Microstomum papillosum Graff, 1882	1343	m
Microstomum bioculatum Faubel, 1984	7061	g
Prolecitophora		
Archimonotresis limophila Meixner, 1938	38	g
Proseriata		
Archilopsis unipunctata Fabricius, 1928	83	p
Promonotus schultzei Meixner, 1943	512	p
Typhloplanoida		
Haloplanella minuta Luther, 1946	25	p
Promesostoma gracilis Ax, 1951	322	p
Promesostoma rostratum Ax, 1951	22	p
Promesostoma karlingi Ehlers, 1974	8	p
Promesostoma meixneri Ax, 1951	1	p
Promesostoma marmoratum (Schultze, 1851)	9	p
Promesostoma caligulatum Ax, 1952	38	p
Messoplana elegans (Luther, 1948)	1	p
Messoplana spec. 1	1	
Ptychoptera westbladi Luther, 1943	5	p
Proxenetes quinquespinosus Ax, 1951	316	p
Proxenetes quadrispinosus Den Hartog, 1966	343	p
Proxenetes intermedius Den Hartog, 1966	42	p
Proxenetes segmentatus Den Hartog, 1966	148	p
Proxenetes ampullatus Ax, 1971	1	p
Proxenetes trigonus Ax, 1971	1	p
Kalyptorhynchia		
Acrorhynchides robustus Karling, 1931	23	p
Scanorhynchus forcipatus Karling, 1955	5	p
Danorhynchus duplostylis Karling, 1955	1	p
Phonorhynchus helgolandicus (Mezcnikoff, 1865)	1	p
Zonorhynchus seminascatus Karling, 1956	58	p
Zonorhynchus salinus Karling, 1952	4	p
Placorhynchus octaculeatus (Karling, 1947)	106	p
Placorhynchus dimorphis (Karling, 1947)	7	p
Placorhynchus spec. 1	1	p
Neognathorhynchus lobatus (Ax, 1952)	1	p
Psittacorhynchus verweyi Den Hartog, 1968	285	p
Schizorhynchia indet.	2	p
Dalyellioida		
Bresslauilla relicta Reisinger, 1929	214	g
Halammovortex macropharynx Meixner, 1938	36	p
Provortex tubiferus Luther, 1948	2	g
Pogaina suecica (Luther, 1948)	6325	g
Pseudograffilla arenicola Meixner, 1938	9	p
Baicalellia brevituba Luther, 1921	2	g

coexisting on the mud flat. Three of the species we encountered are still undescribed. They belong to the genera *Messoplana* and *Placorhynchus*, and one to the Schizorhynchia.

40	g
1343	m
7061	g
38	g
83	p
512	p
25	p
322	p
22	p
8	p
1	p
9	p
38	p
1	p
1	
5	p
316	p
343	p
42	p
148	p
1	p
1	p
23	p
5	p
1	p
1	p
58	p
4	p
106	p
7	p
1	p
1	p
285	p
2	p
214	g
36	p
2	g
6325	g
9	p
2	g

countered are still un-
icorhynchus, and one to

2. Abundance

The mean abundance of 260 individuals · 10 cm^{-2} is calculated from a total of 120 samples (3.8 cm^2/0–1.5 cm), taken in November 1982, February and May 1983. Total abundance was lowest in autumn and highest in spring (Table 3). In

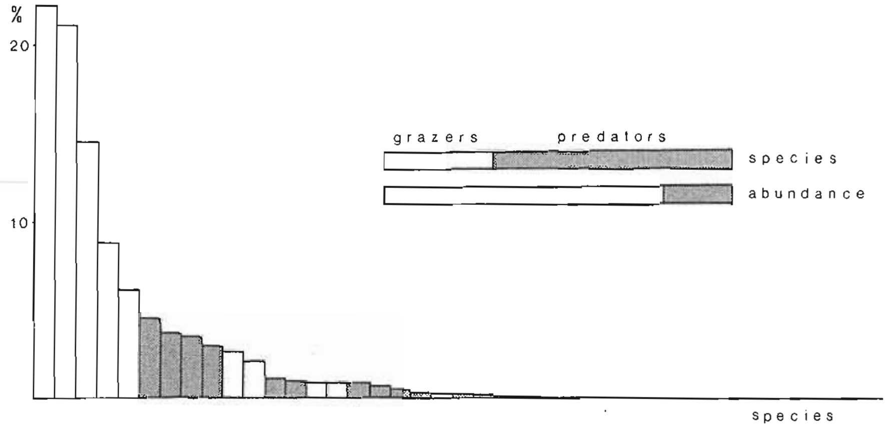

Fig. 2. Rank-order of abundance of 42 species of Plathelminthes; percentages are 3-months averages. White columns are predominantly grazers, shaded columns predators. Horizontal bars give proportions of grazers to predators.

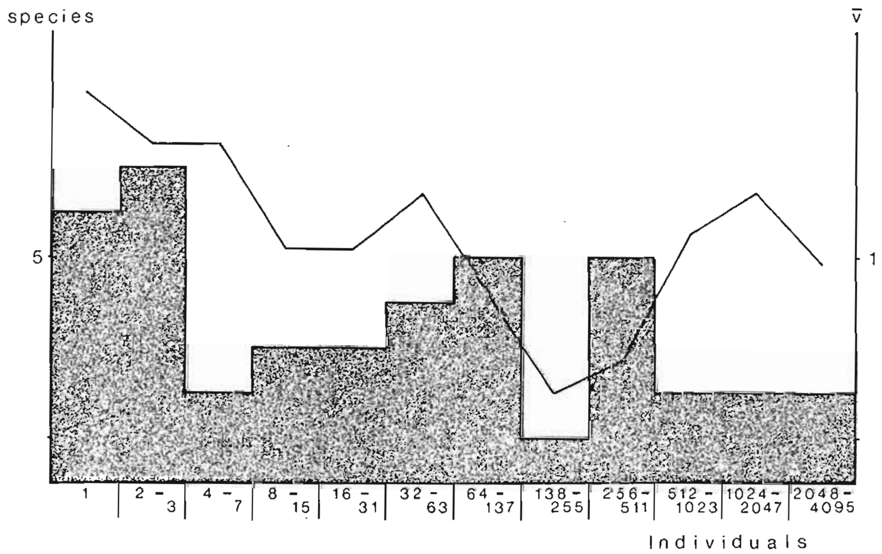

Fig. 3. Geometrical classes of species abundances (columns) and temporal variability within classes of abundance (straight line), Plathelminthes on the mud flat in November 1982, February and May 1983.

Table 3: Abundance (individuals below 10 cm^2) of plathelminth species on a mud flat in Königshafen, isle of Sylt. Each month 40 samples of 3.8 cm^2/0–1.5 cm were taken; v is the coefficient of variation (s / x̄) between months. Juveniles were alloted in proportion between species where only adults were identifiable on species level.

species	Nov. 1982	Febr. 1983	May 1983	mean	%	v
all individuals	96.70	306.10	375.80	259.50	100.00	.56
Microstomum bioculatum	5.01	4.67	163.75	57.81	22.28	1.58
Pogaina suecica	39.09	77.04	47.76	54.63	21.05	.36
Archaphanostoma agile	.13	63.09	50.07	37.76	14.55	.88
Microstomum papillosum	.00	68.16	.59	22.92	8.83	1.71
Philactinoposthia saliens	.89	13.55	33.75	16.06	6.19	1.03
Proxenetes quinquespinosus	6.61	27.83	1.32	11.92	4.59	1.18
Proxenetes quadrispinosus	2.82	6.84	18.55	9.40	3.62	.87
Promesostoma gracilis	15.53	6.71	4.41	8.79	3.39	.68
Promonotus schultzei	3.92	8.68	10.00	7.53	2.90	.42
Pseudaphanostoma brevicaudatum	3.59	7.47	9.21	6.76	2.61	.43
Mecynostomum auritum	7.19	5.99	3.55	5.58	2.15	.33
Proxenetes segmentatus	1.54	3.22	3.68	2.81	1.08	.40
Psittacorhynchus verweyi	.83	2.30	4.41	2.51	.97	.72
Pseudaphanostoma pelophilum	1.79	3.42	1.91	2.37	.91	.38
Bresslauilla relicta	.96	2.17	3.42	2.18	.84	.56
Philachoerus johanni	.00	.26	6.25	2.17	.84	1.63
Archilopsis unipunctata	.32	1.32	3.36	1.67	.64	.93
Placorhynchus octaculeatus	.83	.79	2.30	1.31	.50	.66
Proxenetes intermedius	.00	.00	2.83	.94	.36	1.73
Macrostomum pusillum	2.18	.39	.13	.90	.35	1.24
Promesostoma rostratum	1.86	.07	.13	.69	.27	1.48
Promesostoma caligulatum	.00	.00	1.71	.57	.22	1.73
Zonorhynchus seminascatus	.06	.53	.86	.48	.18	.83
Haloplanella minuta	.45	.53	.13	.37	.14	.57
Archimonotresis limophila	.00	.13	.59	.24	.19	1.29
Ptychoptera westbladi	.13	.13	.26	.17	.07	.43
Acrorhynchides robustus	.00	.07	.46	.18	.06	1.40
Pseudaphanostoma psammophilum	.45	.00	.00	.15	.06	1.73
Halammovortex macropharynx	.00	.07	.33	.13	.05	1.30
Pseudograffilla arenicola	.00	.07	.13	.07	.03	.98
Promesostoma karlingi	.19	.00	.00	.06	.02	1.73
Proxenetes trigonus	.19	.00	.00	.06	.02	1.73
Zonorhynchus salinus	.00	.07	.07	.05	.02	.87
Scanorhynchus forcipatus	.00	.13	.00	.04	.02	1.73
Proxenetes ampullatus	.00	.00	.13	.04	.02	1.73
Baicalellia brevituba	.00	.13	.00	.04	.02	1.73
Anaperus tvaerminnensis	.00	.07	.00	.02	.01	1.73
Praeaphanostoma chaetocaudatum	.00	.07	.00	.02	.01	1.73
Placorhynchus spec. 1	.06	.00	.00	.02	.01	1.73
Danorhynchus duplostylis	.06	.00	.00	.02	.01	1.73
Gnathorhynchus lobatus	.00	.07	.00	.02	.01	1.73
Schizorhynchia indet.	.00	.00	.07	.02	.01	1.73

on a mud flat in Königsha-
ıken; v is the coefficient of
between species where only

mean	%	v
259.50	100.00	.56
57.81	22.28	1.58
54.63	21.05	.36
37.76	14.55	.88
22.92	8.83	1.71
16.06	6.19	1.03
11.92	4.59	1.18
9.40	3.62	.87
8.79	3.39	.68
7.53	2.90	.42
6.76	2.61	.43
5.58	2.15	.33
2.81	1.08	.40
2.51	.97	.72
2.37	.91	.38
2.18	.84	.56
2.17	.84	1.63
1.67	.64	.93
1.31	.50	.66
.94	.36	1.73
.90	.35	1.24
.69	.27	1.48
.57	.22	1.73
.48	.18	.83
.37	.14	.57
.24	.19	1.29
.17	.07	.43
.18	.06	1.40
.15	.06	1.73
.13	.05	1.30
.07	.03	.98
.06	.02	1.73
.06	.02	1.73
.05	.02	.87
.04	.02	1.73
.04	.02	1.73
.04	.02	1.73
.02	.01	1.73
.02	.01	1.73
.02	.01	1.73
.02	.01	1.73
.02	.01	1.73
.02	.01	1.73

November, the assemblage was dominated by *Pogaina suecica* (40 %) and *Promesostoma gracilis* (16 %). In February 5 species attained a density of > 10 individuals 10 cm^{-2}: *P. suecica, Microstomum papillosum, Archaphanostoma agile, Proxenetes quinquespinosus* and *Philactinoposthia saliens.* In early May (first set of samples), *Microstomum bioculatum* outnumbered all other species with 56 % of the total.

Considering the surveys of the three months together, the rank-order of species abundance shows that this assemblage was strongly dominated by few species (Fig. 2). The three most abundant species (*M. bioculatum, P. suecica, A. agile*) together comprised more than half of the total abundance. On the other hand, 30 species out of 42 remained below 1 % each.

Temporal variability (v in Table 3) from November to May was generally

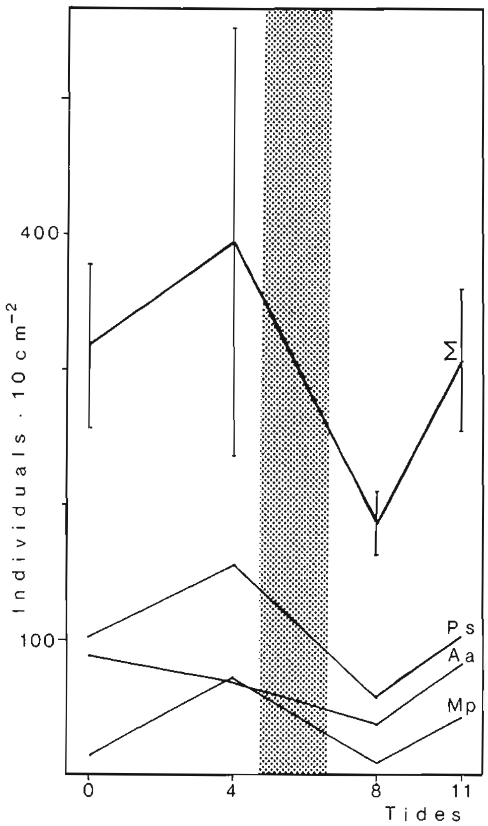

Fig. 4. Abundance (Individuals · 10 cm^{-2}) of Plathelminthes, sampled within a week in March 1983. The shaded area indicates stormy weather. $\sum$ = total assemblage, P s = *Pogaina suecica,* A a = *Archaphanostoma agile,* M p = *Microstomum papillosum.*

high. This was most pronounced in the very abundant species and in the rare species, while moderately abundant species were less variable through time (Fig. 3). The only species remaining among the top most abundant species from autumn to spring was *P. suecica.*

A rough sea caused by strong westerly winds disturbed the plathelminth assemblage of the mud flat (Fig. 4). Abundance decreased by 47 % but pre-disturbance values were quickly re-established. Apparently, plathelminthes were dislocated by the rough sea but subsequently found their way back to the muddy sediment.

3. Trophic Structure

Based on observations on gut content and feeding behavior, species are categorized as predators, grazers and mixed feeders (Table 2). Most species (67 %) prey on other meiofauna. Four are regarded as mixed feeders because they ingest microalgae as well as Foraminifera and copepod nauplii. However, their most frequent identifiable food items were diatoms. This also applies to most other species which are categorized as grazers. Mixed feeders and grazers together far outnumber the predators in terms of individuals. On the average, their share of total abundance is 81 %. All the top most abundant species are either grazers or mixed feeders, while predators prevail at the lower ranks (Fig. 2). Temporal variability is high in both trophic groups (v in Table 3; predators 1.02 ± 0.56, grazers and mixed feeders 1.26 ± 0.50). Considering

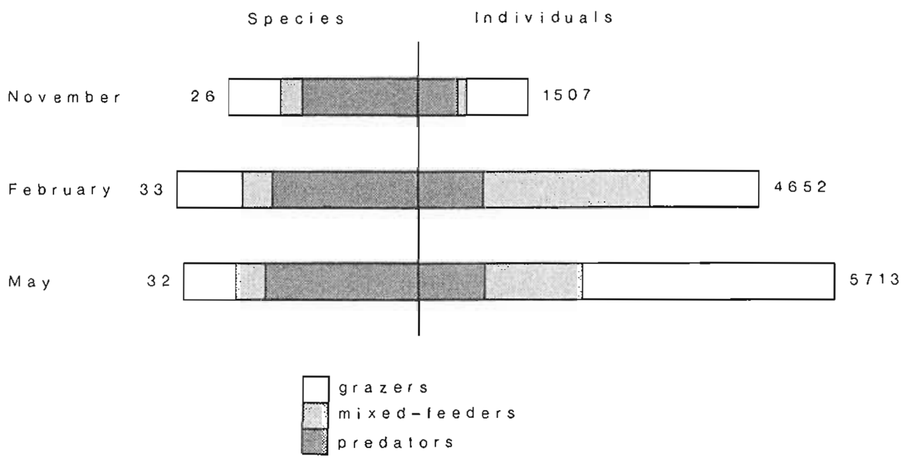

Fig. 5. Distribution of trophic groups over species and individual numbers of a plathelminth assemblage in a mud flat during three investigated months (120 samples of 3.8 cm^2).

absolute numbers, species number within trophic groups showed little temporal variation, while the abundance of grazers and mixed feeders increased considerably from November to May (Fig. 5). Abundance of predators remained fairly constant. In November, a predator (*Promesostoma gracilis*) was the second most abundant species. In February, the predator *Proxenetes quinquespinosus* attained rank 4, and in May *Proxenetes quadrispinosus* was on rank 5. All other top ranks were occupied by grazers and mixed feeders.

4. Spatial Patterns

Although the general appearance of the mud flat is that of a relatively homogeneous habitat, the dispersion of Plathelminthes is patchy. In June 1983, two sets of samples have been taken, one set from a plot of 0.3 m^2, the other set was spread over the entire mud flat (see Fig. 1). The mean (m) and the ratio of variance versus mean (v/m) of the constituent species are plotted logarithmically to detect patterns deviating from randomness (GAGE and GEEKIE 1973). On the 0.3 m^2 scale, only three populations exhibited significant spatial deviations from randomness (Fig. 6, above). On the scale of the entire mud flat, 61 % of all populations departed from random pattern (Fig. 6, below). Predators tend to be more aggregated than grazers or mixed feeders. All plathelminth populations taken together, the pattern was highly aggregated at both scales of investigation.

In November 1982, February and May 1983 samples have been taken from a mud bank which regularly emerges during low tide, and from a muddy depression nearby which remains covered by residual water throughout low tide period. The two sites differed significantly in total abundance, and the lower values were always found at the permanently submerged site. This was most pronounced in November 1982 (mud bank: 158 ± 103, mud depression: 32 ± 23, $p = 0.01$) and early May (mud bank: 969 ± 512, mud depression: 112 ± 96, $p = 0.02$). In November and May most species preferentially populated the mud bank, while in February only two species were significantly more abundant at this site (Table 4). *Promesostoma gracilis* preferred the mud bank in November and the muddy depression in February. The mass development of *Microstomum bioculatum* in May was entirely restricted to the mud bank.

In early summer 1983, mats of macroalgae began to cover parts of the mud flat. The mats were primarily composed of *Ulva lactuca, Fucus vesiculosus* and *Enteromorpha* spp. Pieces of 10 cm^2 were cut out of these mats and analyzed with respect to plathelminth species composition and abundance. The species assemblage was essentially the same compared to the bare mud next to the algal mats. Abundance was highly variable ($\bar{x} = 78 \pm 135$ individuals $\cdot$ 10 cm^{-2}) but no

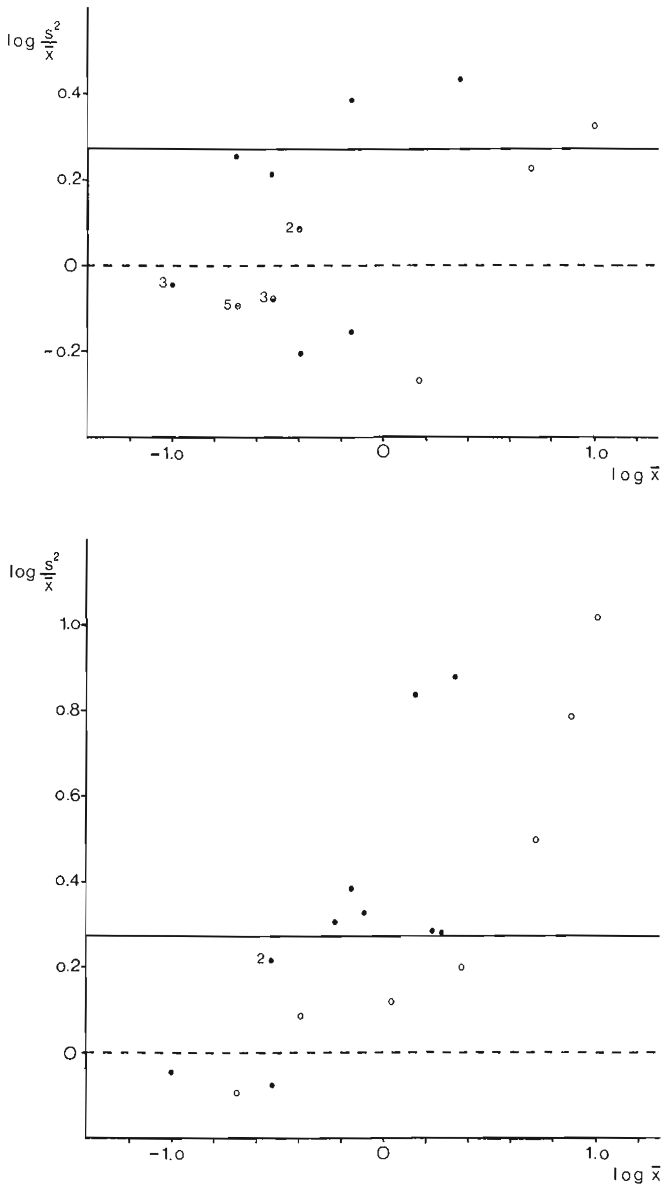

Fig. 6. Logarithmic scatter diagrams of variance-to-mean ratio versus mean, calculated for species populations from sets of 10 samples taken from a 0.3 m^2 plot (above) and from the entire mud flat (below) in June 1983. Broken line marks randomness ($\bar{x} = s^2$), solid line marks upper limit of random expectation ($P = 0.95$). Open circles are grazers or mixed feeders, dots are predators. Numbers refer to more than one point in the same position, if feeding types fall together, the open circle is filled with a dot.

Table 4. Differential abundance of Plathelminthes in a permanently submerged muddy depression and on a mud bank subject to tidal exposure. Sets of 20 samples (3.8 cm^2/0–1.5 cm) were taken from each of the two sites and compared in the three months. Only abundant species are included (see Table 3.).

U-test after Wilcoxon, Mann & Whitney	November 1982	February 1983	May 1983
no difference between sites ($P > 0.05$)	*Philactinoposthia saliens* *Promonotus schultzei*	*Microstomum bioculatum* *Pogaina suecica* *Archaphanostoma agile* *Philactinoposthia saliens* *Proxenetes quinquespinosus* *P. quadrispinosus* *Promonotus schultzei* *Mecynostomum auritum* *Proxenetes segmentatus* *Psittacorhynchus verweyi*	*Proxenetes quinquespinosus* *P. quadrispinosus* *Promesostoma gracilis*
more abundant on mud bank ($P < 0.05$)	*Microstomum bioculatum* *Pogaina suecica* *Proxenetes quinquespinosus* *P. quadrispinosus* *Promesostoma gracilis* *Pseudaphanostoma brevicaudatum* *Mecynostomum auritum* *Proxenetes segmentatus* *Psittacorhynchus verweyi*	*Microstomum papillosum* *Pseudaphanostoma brevicaudatum*	*Microstomum bioculatum* *Pogaina suecica* *Archaphanostoma agile* *Philactinoposthia saliens* *Promonotus schultzei* *Pseudaphanostoma brevicaudatum* *Mecynostomum auritum* *Proxenetes segmentatus* *Psittacorhynchus verweyi*
More abundant in muddy depression ($P < 0.05$)		*Promesostoma gracilis*	

significantly different values were obtained from bare mud ($\bar{x} = 135 \pm 50$). *Pogaina suecica* and *Philactinoposthia saliens* were almost absent within the algal mats but very abundant on the bare mud. No species showed a significant preference for the algal mats. Only juvenile Acoela attained occasionally high numbers.

On the mud flat, Plathelminthes are essentially benthic species. At low tide, 10 l of overlying water were skimmed off with a beaker in the lagoon area. Only 12 individuals were found, 7 belonging to *Microstomum bioculatum*.

5. Size and Biomass

The mud flat was dominated by very small sized Plathelminthes (Fig. 7). Of all individuals, 90 % were smaller than 1 mm in length, and most of these even less than 0.5 mm.

From these length measurements, a rough estimate of biomass is possible, using determinations of dry weight by FAUBEL (1982). The biomass of Plathelminthes in the mud was approximately 0.15 g dry weight m^{-2}. WIDBOM (1984) found that the ash-free weight in Plathelminthes amounts to 78 % of dry weight. Thus, the biomass in terms of organic dry weight on the mud flat was about 0.12 g m^{-2}. The individuals less than 1 mm length accounted for 80 % of the biomass (Fig. 7).

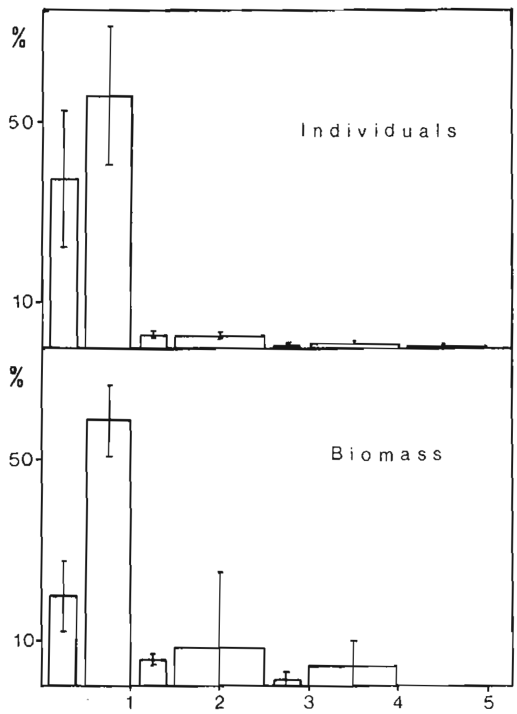

Fig. 7. Percentage distribution of individuals and biomass over size classes of Plathelminthes averaged from three months. The size classes are chosen in accordance with FAUBEL (1982) to perform the conversion to biomass in terms of dry weight.

D. Discussion

1. Species Composition

RIEDL (1956) documented the prevalence of Acoela in muddy marine sediments, and DÖRJES (1968) and FAUBEL (1977) mention a high number of acoel species living in muddy habitats in the North Sea, including the Königshafen at the isle of Sylt. In the present study, Acoela comprise 9 out of 49 species and 27 % of total abundance. *Archaphanostoma agile* and *Philactinoposthia saliens* belong to the ten most abundant species. However this assemblage is not dominated by Acoela as RIEDL (1956) found for muddy bottoms of the Adria and Skagerak. Most species belong to the Neorhabdocoela, and the Macrostomida comprise 31 % of all individuals.

Except for a still undescribed species of the genus *Messoplana* which was found in the algal mats, all species recorded on the mud flat have also been found elsewhere in Königshafen (ARMONIES and HELLWIG, in prep., REISE 1984 and unpublished records). This suggests that mud-dwelling Plathelminthes are more habitat generalists than specialists. Some of the dominant species, however, apparently show a preference for the mud flat region: *Archaphanostoma agile, Philactinoposthia saliens, Mecynostomum auritum, Pseudaphanostoma brevicaudatum, Pseudaphanostoma pelophilum, Microstomum bioculatum* and *Pogaina suecica.* These species occur also in salt marshes, seagrass beds or sandy flats but are most abundant on the mud flat.

2. Abundance and Diversity

Published records on Plathelminthes in shallow, muddy sediments are rare, and often they appear to be absent. MONTAGNA et al (1983) investigated the meiofauna of a mud site in the North Inlet Estuary (South Carolina) and found 18 ± 8 Plathelminthes · 10 cm^{-2}, corresponding to 3.8 % of total meiofauna. On a mud flat in Tamar Estuary (England), ELLISON (1984) recorded 1025 Plathelminthes in 44 g wet sediment, which is equivalent to about 280 · 10 cm^{-2} and 5.3 % of total meiofauna. BOUWMAN et al (1984) sampled the meiofauna on organically polluted estuarine mud flats (Eems-Dollard Estuary). From their Fig. 3 an average density of 160 Plathelminthes 10 cm^{-2}, corresponding to 3 % of total meiofauna, can be estimated. At one station they observed a mass development during June – July with a density of up to 1360 · 10 cm^{-2}.

On the mud flat we investigated, 260 · 10 cm^{-2} were found, corresponding to 9–15 % of total meiofauna. Thus, abundance of Plathelminthes in muddy sediments ranges from none (i. e. REES 1940, WARWICK et al 1979) to about 300 · 10 cm^{-2}. The short term mass development observed by BOUWMAN et al (1984) indicates that Plathelminthes are a fluctuating component of the mud flat meiofauna. However, further variation in the published records is possibly an artifact of the extraction procedure applied to get meiofauna out of the mud. According to MARTENS (1983), Plathelminthes are very difficult to identify as such in preserved material. Whenever possible, Plathelminthes should be extracted and sorted while still alive.

Table 5: Comparison of some characteristics of the plathelminth assemblages occurring on a sand flat (REISE 1984) and a mud flat in Königshafen, isle of Sylt.

Plathelminth assemblage	sand flat	mud flat
mean abundance 10 cm^{-2}	111	260
number of species 10 cm^{-2}	24	14
Total number of species	83	49
abundance of predators (%)	53	19
Shannon's diversity $H = - \sum p_i \ln p_i$	3.35	2.10
Mean length of individuals (mm)	1.06	0.45

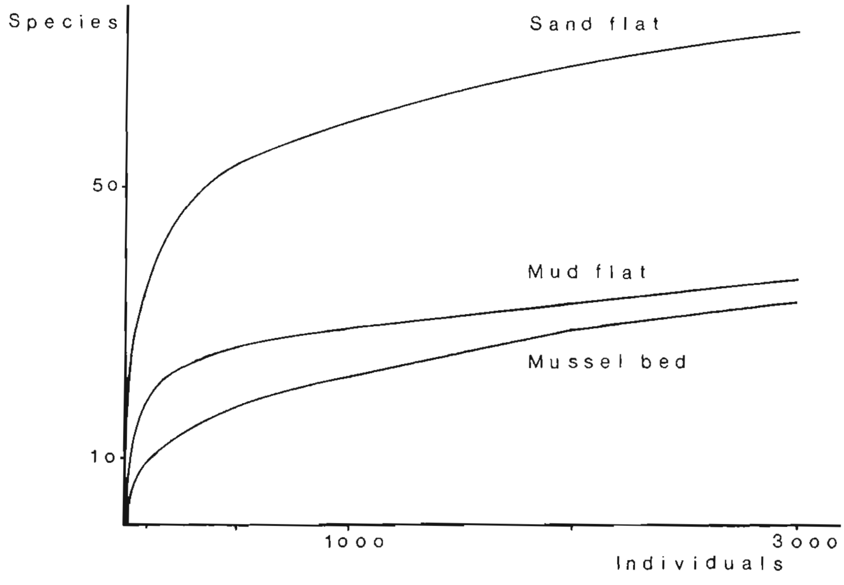

Fig. 8. Arithmetical plot of the number of species at different population sizes using the rarefaction methodology of Sanders (1968) to compare the diversity of plathelminth assemblages from a sand flat, a mud flat and a muddy mussel bed (*Mytilus edulis L.*) in Königshafen, isle of Sylt.

Compared to an adjacent sand flat in Königshafen, the plathelminth assemblage of the mud flat comprises more individuals but less species (Table 5). Diversity is higher in sand than in mud (Fig. 8). This is in accordance with the distribution of other meiofaunal groups in sand and mud (COULL and BELL 1979). In mud, only the upper few mm of sediment are inhabitable to Plathelminthes. Below a flaky and semi-fluid surface layer, the mud flat sediment was firm and anoxic. Thus, the mud flat assemblage lacks a vertical habitat dimension. On the sand flat, there are several distinct microhabitats below the sediment surface and these are differentially utilized by the plathelminth species (REISE 1984). These microhabitats may serve as refuges when conditions at the surface become harsh, and Plathelminthes are known to perform vertical migrations in sandy sediments in relation to tidal cycles (i. e. MEINEKE and WESTHEIDE 1979, XYLANDER and REISE 1984). The mud flat assemblage has no such refuges at its disposal, and we observed that a rough sea caused a significant decline in abundance (Fig. 4). In calm waters we found low numbers which indicates that these mud-dwelling Plathelminthes are not permanently on the move, as has been shown for copepods by BELL and SHERMAN (1980).

3. Trophic Structure

The mud flat assemblage is dominated by diatom feeders, while predators are more important on the sand flat (Table 5). Production by benthic microalgae (mainly diatoms) is particularly high on intertidal mud flats (COLIJN and DE JONGE 1984). In contrast to many macrophytes (kelp, seagrass) these unicellular algae are directly utilizable by benthic consumers and constitute an important food source on the muddy flats (ADMIRAAL et al 1983, PETERSON 1981). On an estuarine mud flat in the Dollart, most of the meiofaunal organisms fed on benthic diatoms (BOUWMAN et al 1984), and REES (1940) recorded highest meiofaunal densities where most diatoms occurred. MONTAGNA et al (1983) found a positive correlation between plathelminth and diatom abundance at a mud site but not in sand. We suggest that the plathelminth assemblage on muddy intertidal flats are principally diatom based, and that this pathway is echoed by high population densities.

4. Adaptations to Life in Mud

Meiofauna in mud lacks the morphological features characteristic of the interstitial fauna of sandy sediments (FENCHEL 1978). Elongated body shape or small size to fit into the interstices of sand, and adhesive organs to prevent dislocation when current velocities or waves are strong (Ax 1966), are not called for in the soft mud lacking interstices and there are no solid particles to attach to. Coull and Bell (1979) suggest that mud dwellers are not restricted to a particular shape and are generally larger than sand dwellers. This is not true for the Plathelminthes. They are smaller in mud than in sand (Table 5). Dörjes (1968) observed that Acoela living in mud are short and compact. This also holds for most other plathelminths we found on the mud flats.

The conspicious mass development of *Microstomum bioculatum* on the mud flat in May (see also Faubel 1984), and a similar observation for Plathelminthes on another mud flat (Bouwman et al 1984), does not suggest a competitive assemblage regulated by crowding effects close to its carrying capacity. The dominant species on the mud flat show attributes characteristic for r-selection (see May 1976, Parry 1981). The two *Microstomum* species, *M. bioculatum* and *M. papillosum* produce rapidly through paratomy. Abundance of *M. bioculatum* increased by 300 % within a week. This coincided with a mass development of the diatom *Gyrosigma* sp. *Archaphanostoma agile* (and other Acoela) is capable of continous egg production and average generation time under laboratory conditions is only 23 days (Apelt 1969). The main food source of the dominant species, the diatoms, are well known for short-term mass developments (spring: Asmus 1982, summer: Admiraal and Peletier 1980; autumn: Schwinghamer1983). Variability of resources and lack of refuges in the vertical dimension of the sediment are likely to be responsible for a highly unstable plathelminth assemblage in the intertidal mud flat.

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Zusammenfassung

Die Besiedlung eines strömungsgeschützten Schlickwattgebietes im Königshafen der Nordseeinsel Sylt durch freilebende Plathelminthen (Turbellarien) wurde von Oktober 1982 bis Juni 1983 untersucht. In den Monaten November 1982, Februar und Mai 1983 wurden jeweils 40 Proben (3.8 cm^2/0–1.5 cm Tiefe)

genommen. Zwischenzeitlich erfolgten ergänzende Probenahmen zur Aufdekkung räumlicher Verteilungsmuster.

Im Vergleich zum benachbarten Sandwattgebiet ist im Schlick die mittlere Abundanz (260 Individuen · 10 cm^{-2}) sehr hoch, während die Artenzahl (insgesamt 49 und 14 auf 10 cm^2) und die Diversität (H = 2.10) relativ gering ist. Folgende Arten besiedeln bevorzugt die Schlicksedimente: *Microstomum bioculatum, Pogaina suecica, Archaphanostoma agile, Philactinoposthia saliens, Mecynostomum auritum, Pseudaphanostoma brevicaudatum* und *Pseudaphanostoma pelophilum*. Die Besiedlung wird von wenigen, sehr häufigen Arten dominiert (5 Arten stellen 73 % der Abundanz), deren Populationen zeitlich stark schwanken. Alle häufigen Arten sind Diatomeenfresser (81 % der Individuen) und ihre Abundanz nahm vom Herbst zum Frühjahr beträchtlich zu. Alle räuberischen Plathelminthen (67 % der Arten) besetzen die unteren Ränge im Abundanzspektrum.

Die räumliche Verteilung der Populationen erscheint auf kleiner Fläche (0.3 m^2) vorwiegend zufällig, während im gesamten Schlickwattbereich 61 % der Populationen geklumpt verteilt sind. Eine ständig wasserbedeckte Schlicksenke ist weniger dicht von Plathelminthen besiedelt als die im Tidenrhythmus auftauchende Schlickbank. Die Abundanz innerhalb der Matten aus Makroalgen variiert sehr, ist aber nicht signifikant verschieden vom umgebenden Sediment. Die meisten Plathelminthen im Schlick sind auffällig klein (90 % < 1 mm, mittlere Länge 0,45 mm). Die Biomasse beträgt nur 0,15 g m^{-2}.

Die hohen Fluktuationen in der Besiedlung des Schlickwatts sind vermutlich begründet in dem wechselhaften Nahrungsangebot (vornehmlich Diatomeen) und fehlenden Rückzugsmöglichkeiten von der Schlickoberfläche in tiefere Schichten, wenn sich die Lebensbedingungen verschlechtern.

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