

## Semiplanktonic Plathelminthes in the Wadden Sea

W. Armonies

Biologische Anstalt Helgoland (Litoralstation), D-2282 List, FRG

### Abstract

Traditionally benthic Plathelminthes were thought to be restricted to life in the sediment. However, recent studies revealed that many species may actively enter the water column. Experiments and field distribution data of Plathelminthes from an intertidal sandflat of the northern Wadden Sea (North Sea) in summer 1987 and 1988 are used to evaluate the specific composition of active swimmers and non-swimmers. It is shown that life-style changes continuously – from entirely benthic to semiplanktonic. With respect to swimming activity, phytal species connect semiplanktonic and entirely planktonic species. Morphology and ecology change in parallel to life-style. Consequently, the active swimming potential of Plathelminthes should be taken into account in both descriptive and experimental studies.

### Introduction

Pelagic species of Plathelminthes are well known, e.g. Polycladida (Faubel 1984), Prolecithophora (Westblad 1955), Acoela (Löhner and Micoletzky 1911), or the macrostomid *Alaurina composita* Metschnikow. On the other hand, there are some thousands of species which are traditionally thought to be confined to the sediment. However, submergence experiments on intertidal sediment showed that significant numbers of meiobenthos may actively enter the water column. Among these actively swimming meiobenthos, harpacticoid copepods and Plathelminthes were the dominant taxa (Armonies 1988a). Further studies revealed that swimming in the water column is strongly dependent upon physical factors such as light intensity, current speed, temperature, oxygen, and salinity (Armonies 1988b, c). Light intensity and current speed affected all species in a similar way, while the effect of the other factors seems to be species specific. Decreased light intensity increases the number of swimmers, although the percentage of swimmers in a popu-

lation is also species specific (Walters and Bell 1986, Armonies 1988b, Walters 1988). Flow exerts a non-linear effect. The number of swimmers is high in low flow, drops to a minimum as flow increases, and increases again as the sediment becomes eroded. In the latter case Nematoda, Gastrotricha, and Oligochaeta are also found in the water column, indicating that both active emergence and passive drift from resuspension contribute to the occurrence of meiobenthos in the water column (Palmer and Gust 1985, Palmer 1986, 1988, Armonies 1988b).

In Plathelminthes, there seems to be some benthic species which never actively leave the sediment. Some species leave the sediment when an environmental factor such as oxygen availability or salinity has, experimentally, deteriorated. Presumably they try to escape the unfavourable conditions. Direct observation of such swimmers in an aquarium shows that they swim 2 to 4 cm above the sediment, maintain that position for a short time, and then actively return to the sediment (Armonies 1988b). In the field, tidal currents disperse them while swimming. A third group of swimmers also left sediment where no physical factors had been changed. Some of them seem to pursue a semiplanktonic way of life: during low-tide and, in part, during daylight, they remain in the superficial sediment layers and at night, actively swim in the water column. Some harpacticoid species such as *Harpacticus flexus* Brady and Robertson and *Tachidius discipes* Giesbrecht show a corresponding interchange between benthic and planktonic life-styles (Armonies 1989).

In most of the above cases, any single laboratory experiment contained too few plathelminths to recognize species-specific behaviour. However, by combining all published (Armonies 1988a, b, c) and yet unpublished data, over 3 000 individuals were obtained. This number seems to be sufficient for a more general evaluation, as presented in this paper. It is argued that the microturbellarians of the Wadden Sea show a continuous change of life-style from benthic species, which never actively leave the sediment, to semiplanktonic species that enter the water column whenever

possible. Some morphological and ecological characteristics can be used to judge life-style.

### Materials and study site

Laboratory experiments were conducted on the swimming behaviour of intertidal meiobenthos (Armonies 1988 a, b, c). The plathelminth data from these studies, as well as new data from laboratory and field experiments, are used to evaluate plathelminth swimming behaviour. For all experiments, samples were collected from a 50 × 50 m plot of the Königshafen Wadden area near the Island of Sylt (North Sea, FRG). For a general description of the area see Reise (1985).

The plot is sheltered and sediment is composed mainly of medium sand (median diam. 315 μm, sorting coefficient 1.5) with moderate amounts of detritus (loss on ignition 0.48%). Experiments were performed between May and October 1987, and March and October 1988. Temperature ranges were as follows: Seawater between 6° and 18°C; shallow waters above the intertidal sandflat between 5° and 25°C; and air temperature from 5° to 22°C. The sampled plot is positioned at the mid-tide level (50 to 60% tidal emersion); average tidal range at the plot is 0.9 to 1.1 m.

Laboratory experiments included submersion of sediment samples into aquaria with filtered water and subsequent monitoring of the number of individuals which actively left the sediment and entered the water column. One sample in each experiment served as control, while an environmental factor (temperature, light intensity, salinity, oxygen, current speed, etc.) was changed in the others. After

submersion, some sediment samples were sorted for remaining specimens. For details on laboratory and field experiments see Armonies (1988 a, b, c, 1989).

Although the study period covered 2 yr and treatments differed, each individual present in an experiment had an equal chance of leaving the sediment as any other. Therefore, it was assumed that the percentage of individuals which left the sediment was an indicator of the swimming activity of that species. Specific swimming activity was estimated, using the equation:

$$R = \frac{Pi(w)}{Pi(s)},$$

where  $R$  is the proportion of the percent abundances of species  $i$  related to the total number of Plathelminthes in the water column ( $Pi(w)$ ) and in the sediment ( $Pi(s)$ ), respectively. Note, percentages are individually calculated for water column and sediment samples. Provided all species of Plathelminthes were equally active in swimming, then their percentages in the water column and sediment should also be equal, and  $R$  approach unity. However, swimming activity varied strongly between species (see below). Some seemed to live entirely in the benthos, and their abundance in the water column was zero. On the other hand, very active swimmers contribute to a higher proportion of Plathelminthes in the water column than in the sediment. Given such species specific differences, an  $R \approx 1$  indicated a species of average swimming activity, and  $R \ll 1$  and  $R \gg 1$  less and more active swimmers, respectively.

Correlations between specific swimming activity (as estimated by  $R$ ) and morphological and ecological characters such as body pigmentation or feeding-type were analysed using contingency tables and Chi-square tests on the independence of two variables (Sachs 1984) were performed. Data on specific morphological and ecological characters were compiled from Meixner (1938), Luther (1948), Ax (1951 a, b, 1952, 1956, 1960, 1970, 1971), Karling (1952, 1955, 1956, 1963, 1974), Dörjes (1968), Pawlak (1969), Ax and Heller (1970), Sopott (1972, 1973), Ehlers (1974), Faubel (1974), Reise (1984), Dittmann and Reise (1985), Noldt (1985), Armonies (1986 b, 1987, and unpublished observations), Hellwig (1987), as well as some unpublished reports.

## Results

### Taxonomic composition

Laboratory experiments (Armonies 1988 a, b, c, and unpublished) yielded a total of 2 674 Plathelminthes swimming in the water column above experimentally submerged sediment, and 649 individuals resting in the sediment after experimental submergence, representing a total of 43 species (Table 1). The combined Macrostomida, Proseriata and Kalyptorhynchia percentages in the water column were less than half that of the sediment. The converse was for Typhloplanoida, indicating that this taxon contained some excellent swimmers. Above all, *Promesostoma marmoratum* and

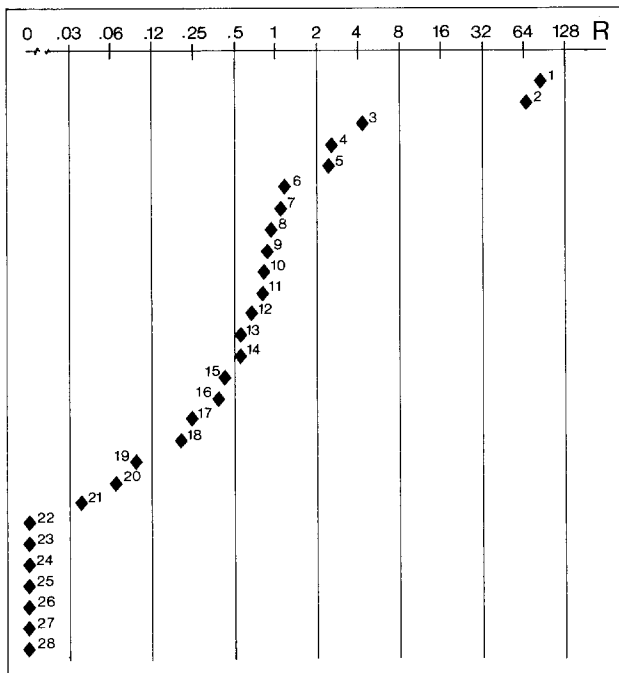


Fig. 1. Plathelminth species from an intertidal sandflat near the Island of Sylt, FRG. Log-scale distribution of swimming activity ( $R$ ) for the 28 most abundant species (denoted as in Table 1)

**Table 1.** Plathelminth species from an intertidal sand flat near the Island of Sylt, FRG. Numbers (*N*) and respective percentages (%) of individuals found either swimming (Water column) or resting in the sediment after submersion (Sediment). *R*: ratio of swimmers to non-swimmers (see text); Rank: rank order of species according to *R*

Taxon	Water column		Sediment		<i>R</i>	Rank
	<i>N</i>	%	<i>N</i>	%		
<b>Acoela</b>						
<i>Anaperus tvaerminnensis</i> (Luther, 1912)	23	0.86	7	1.08	0.80	11
<i>Pseudaphanostoma psammophilum</i> Dörjes, 1968 *	114	4.26	34	5.24	0.81	10
<i>Postmecynostomum pictum</i> Dörjes, 1968	8	0.30	8	1.23	0.24	17
<b>Macrostomida</b>						
<i>Macrostomum pusillum</i> Ax, 1951 *	67	2.51	43	6.63	0.38	16
<i>Microstomum jenseni</i> Riedl, 1932	75	2.81	21	3.24	0.87	9
<i>Paromalostomum dubium</i> (De Beauchamp, 1927)	0	0	5	0.77	0	27
<i>Paromalostomum fuscum</i> Ax, 1957	0	0	1	0.15	0	34
<b>Proseriata</b>						
<i>Archiloea petiti</i> Ax, 1956	6	0.22	21	3.24	0.07	20
<i>Archilopsis arenaria</i> Martens nom. nud.	46	1.72	12	1.85	0.93	8
<i>Archilopsis inopinata</i> Martens nom. nud.	1	0.04	0	0		41
<i>Monocelis lineata</i> O. F. Müller, 1774	1	0.04	0	0		42
<i>Coelogygnopora axi</i> Sopott, 1972	0	0	1	0.15	0	35
<b>Dalyellioida</b>						
<i>Pogaina suecica</i> (Luther, 1948) *	1 019	38.10	101	15.56	2.45	5
<i>Pogaina kinnei</i> Ax, 1970 *	201	7.52	115	17.72	0.42	15
<i>Provortex tubiferus</i> Luther, 1948 *	108	4.04	23	3.54	1.14	6
<i>Provortex psammophilus</i> Ax, 1951	15	0.56	18	2.77	0.20	18
<i>Bresslauilla relicta</i> Reisinger, 1929	8	0.30	50	7.70	0.04	21
<i>Pseudograffilla arenicola</i> Meixner, 1938	9	0.34	4	0.62	0.55	14
<i>Halammovortex macropharynx</i> (Meixner, 1938)	0	0	1	0.15	0	36
<i>Drepanilla</i> spec.	0	0	2	0.31	0	33
<b>Typhloplanoida</b>						
<i>Promesostoma caligulatum</i> Ax, 1952 *	343	12.83	1	0.15	85.53	1
<i>P. gracilis</i> Ax, 1951	3	0.11	0	0		40
<i>P. karlingi</i> Ehlers, 1974	17	0.64	1	0.15	4.27	3
<i>P. marmoratum</i> (M. Schultze, 1851) *	266	9.95	1	0.15	66.33	2
<i>P. meixneri</i> Ax, 1951	271	10.13	26	4.01	2.53	4
<i>P. rostratum</i> Ax, 1951	3	0.11	0	0		39
<i>Pratoplana salsa</i> Ax, 1960	1	0.04	0	0		43
<i>Proxenetes quinquespinosus</i> Ax, 1971	0	0	10	1.54	0	25
<i>P. quadrispinosus</i> Den Hartog, 1966	0	0	6	0.92	0	26
<i>P. trigonus</i> Ax, 1960	0	0	2	0.31	0	32
<b>Kalyptorhynchia</b>						
<i>Acorrhynchides robustus</i> (Karling, 1931)	9	0.34	4	0.62	0.55	13
<i>Gyatrix hermaphroditus</i> Ehrenberg, 1831	11	0.41	4	0.62	0.66	12
<i>Cheliplanella remanei</i> (Meixner, 1928) *	35	1.31	8	1.23	1.07	7
<i>Cheliplanella caudata</i> Meixner, 1938 *	14	0.52	36	5.57	0.09	19
<i>Zonorhynchus seminascatus</i> Karling, 1956	0	0	22	3.39	0	23
<i>Cicerina brevicirrus</i> Meixner, 1928	0	0	14	2.16	0	24
<i>Ptylacorhynchus coecus</i> Ax, 1951	0	0	3	0.46	0	29
<i>Psammorhynchus tubulipenis</i> Meixner, 1938	0	0	3	0.46	0	30
<i>Psittacorhynchus verweyi</i> Den Hartog, 1968	0	0	1	0.15	0	37
<i>Neoschizorhynchus parvostro</i> Ax & Heller, 1970	0	0	31	4.78	0	22
<i>Typhlorhynchus syltensis</i> Noldt, 1985	0	0	5	0.77	0	28
<i>Karkiorhynchus bruneti</i> Schilke, 1970	0	0	1	0.15	0	38

\* Species found also in field water column samples

*P. caligulatum* were very abundant in the water column (66 and 85 times more so, respectively) while just one individual each was found resting in sediment after submersion.

Water column sampling in the field in summer of 1988 (see Armonies 1989) yielded nine species (Table 1). These were either very active swimmers like the above *Promesos-*

*toma* species, or less active swimmers but occurring in high abundance.

#### Continuous life-style change

Seventeen plathelminth species found in the sediment were never seen in the water column, this may in part be due to

**Table 2.** Plathelminth species contingency table. Variables are body pigmentation (strong, weak, none) and swimming activity ( $R$ ).  $DF=6$ ,  $\chi^2=20.68$ ,  $P<0.01$

Body pigmentation	Swimming activity			
	$R<0.1$	$0.1<R<1$	$1<R<10$	$R>10$
Strong	0	1	2	2
Weak	1	6	2	0
None	9	4	1	0

**Table 3.** Plathelminth species contingency table for the variables presence/absence of eye pigmentation and swimming activity ( $R$ ).  $DF=3$ ,  $\chi^2=4.34$ ,  $P>0.2$

Pigmented eyes	Swimming activity			
	$R<0.1$	$0.1<R<1$	$1<R<10$	$R>10$
Present	4	6	2	4
Absent	6	5	1	0

**Table 4.** Plathelminth species contingency table. Variables are preferred sediment layer at low tide and swimming activity during high tide ( $R$ ).  $DF=6$ ,  $\chi^2=13.3$ ,  $P<0.05$

Position in sediment	Swimming activity			
	$R<0.1$	$0.1<R<1$	$1<R<10$	$R>10$
Surface only	1	7	3	2
Surface and subsurface	5	4	2	0
Subsurface only	4	0	0	0

**Table 5.** Plathelminth species contingency table for the variables feeding-type and swimming activity ( $R$ ).  $DF=9$ ,  $\chi^2=28.52$ ,  $P<0.001$ . Three species were excluded due to lack of reliable food data

Plathelminth feeding-type	Swimming activity			
	$R<0.1$	$0.1<R<1$	$1<R<10$	$R>10$
Copepod-feeders	1	2	3	2
Diatom-feeders	0	6	2	0
Non-specific predators	0	2	0	0
Nematode- and bacteria-feeders	7	0	0	0

low abundance. Since more water samples were analysed the total number of Plathelminthes found in the water column was about 4-fold higher than the number remaining in the sediment. By omitting species with  $<5$  individuals the species list was reduced to 28 'more abundant' species. Of these, ten were rarely, or never, found in the water column ( $R<0.1$ ), and two were far more abundant in the water column than in the sediment ( $R>10$ ). Sixteen species of intermittent swimming behaviour connected both groups,

thus yielding a continuous change in swimming activity (Fig. 1). This change was also maintained, when only species with  $>10$ ,  $>20$ ,  $>50$  or even  $>100$  individuals (according to Table 1) were considered.

#### Ecological and morphological estimators of swimming activity

*Promesostoma marmoratum* and *P. caligulatum* were the most active swimmers (highest  $R$ -values), and both possess brown net-like or striped dorsal pigmentation. Non-swimmers, on the other hand, were usually unpigmented. Furthermore, by arranging the 28 most abundant species into a contingency table, based on body pigmentation and  $R$  values, indicated that the two are not independent (Table 2). Thus, in this sandy intertidal habitat, pigmented species are more active swimmers. However, the presence or absence of pigmented eyes seems to be independent of swimming activity (Table 3).

In the sediment, active swimmers were usually found in the surface layer and non-swimmers in the (still oxic) subsurface layer. However, not all surface dwellers proved to be active swimmers and thus, the correlation between preferred sediment layer of plathelminths at low tide and swimming activity during high tide was rather weak (Table 4).

The degree of plathelminth swimming activity correlated well with food type. Copepod-feeding plathelminths contain the most active swimmers, followed by diatom-feeders and non-specific predators. Species that feed on bacteria or benthic nematodes were the least active swimmers (Table 5).

Associations between the above morphological and ecological parameters and swimming activity appeared to be limited by the size of individuals. *Pseudograffilla arenicola* only emigrated from shallow dishes with sediment and none was found swimming higher than 3 cm above the sediment. Swimmers were all juveniles  $<1$  mm, and three of the four *P. arenicola* resting in the sediment were adults  $>2$  mm.

Nevertheless, using the estimators body pigmentation, vertical position in the sediment during low tide, and food, the plathelminth fauna of the intertidal sandflat studied can be classified into three groups. (1) Benthic species; rather sluggish individuals, often living in deeper sediment layers; no superficial body pigmentation; mostly feeding on Nematoda or bacteria (i.e., non-evasive prey); this group also encloses the thiobiotic species (see below). (2) Facultative swimmers; more active, usually surface dwelling species; often weakly pigmented; feeding on diatoms, copepods, or non-specific predators. (3) Semiplanktonic species; very active long-term swimmers, during low tide resting in superficial sediment; with a dorsally pigmented body wall and pigmented eye-spots; copepod-feeders.

#### Discussion

Is body pigmentation camouflage for swimmers?

Swimming activity correlates significantly with the intensity of body pigmentation in this intertidal sandflat assemblage of Plathelminthes. All species prefer darkness for swimming,

although there are specific differences in the degree of light tolerated while swimming. The dark brown *Promesostoma* species and the yellowish *Pogaina* species enter the water column at a light intensity of  $10 \mu\text{E m}^{-2} \text{s}^{-1}$ . Weakly pigmented *Macrostomum pusillum* and *Provortex tubiferus* tolerate light of  $1 \mu\text{E m}^{-2} \text{s}^{-1}$ . Finally, unpigmented species only enter the water column at light intensities  $< 0.1 \mu\text{E m}^{-2} \text{s}^{-1}$  (Armonies 1988c). Thus, in a gradient of decreasing light, plathelminths with a dark body pigmentation enter the water column earlier than unpigmented ones. Body colouration might therefore act as camouflage for these meio-benthic swimmers. The occurrence of similar pigmentation in different taxa such as *Promesostoma marmoratum* (Typhloplanoida) and *Provortex tubiferus* (Dalyellioida) as well as various kinds of pigmentation in the same taxon (e.g. symbiotic diatoms in *Pogaina suecica* and epidermal pigmentation in *Provortex tubiferus*, both Dalyellioida) corroborate this assumption (Wicksten 1983).

The intensity of body colouration in many species is rather variable. In *Promesostoma marmoratum* and *P. rostratum* dorsal pigmentation is most intense in muddy and weaker in sandy habitats; it may be completely absent in coarse sand poor in detritus (Ax 1951 a). The same applies to *Provortex tubiferus* and *Monocelis lineata* (Ax 1951 a). It seems that body colouration alters with sediment colour, so that individuals match their background.

Plathelminthes, via ciliary movement, can also display a very steady kind of motion which may be regarded as inherent camouflage. Possibly plathelminths are generally less conspicuous to a visual predator than, e.g. a jumping harpacticoid.

However, the question as to which eye they hide in an open one. Although some epibenthic and pelagic predators are known to feed on meiofauna (e.g. Evans 1983, Reise 1985), soft bodied Plathelminthes are not usually found in the stomach contents of predators. Only Zander and Hartwig (1982) mentioned turbellarians as prey of *Pomatoschistus microps*, which also consume a large number of similar sized harpacticoids.

The purpose of the reddish body pigmentation of some plathelminth species living in the RPD- (redox potential discontinuity-) layer of the sediment is presumably not camouflage. The prevalence of non-pigmented species among non-swimmers suggests that there is no need for camouflage inside the sediment. Boaden (1977) assumes this reddish colouration is due to a respiratory pigment.

Thiobiotic species living below the RPD-layer are presumably entirely benthic. Indeed, even after disturbing the sediment, thiobiotics remain in their environment. New habitats are only reached by migration inside deeper layers of the sediment, without contact with the oxic surface layer (Meyers et al. 1988). Presumably thiobiotic species are the most benthic in the gradient of benthic to planktonic life-styles.

#### Eye pigmentation and trophic groups

No correlation could be found between the presence or absence of pigmented eyes and swimming activity. Never-

theless, all species exhibited greatest activity in the dark (Armonies 1988 a, c), indicating that species lacking eye pigmentation are light sensitive. Furthermore, in the taxon Proseriata, several kinds of unpigmented photoreceptors have been found (Sopott-Ehlers 1984, 1986).

There is a close correlation between swimming activity of plathelminth species and their food type. The most active swimmers (*Promesostoma* spp.) suck copepods out. It is not known if victims are caught in the sediment or in the water column. Possibly, planktonic calanoids are also caught. However, most harpacticoids from this sandflat pursue a semiplanktonic life-style, and up to 90% of them may simultaneously swim in the water column at night (Armonies 1989). On the other hand, bacteria-feeders and predators on nematodes, i.e., non-swimming prey, do not swim. Thus, with respect to swimming activity, plathelminths seem to behave like their favoured prey. From this it may be concluded that food is a potential benefit of active swimming, as has been demonstrated for some harpacticoid species (Decho 1988). Copepod-feeding *Promesostoma* species might pursue their prey, and diatom-feeders may seek sites with high diatom abundance (Decho and Fleeger 1988).

#### Phytoplanktonic Plathelminthes enlarge the life-style range

Some microturbellarians show high abundance in algal mats and seagrass canopies, yet are scarce in sediment (e.g. Hellwig-Armonies 1988). Most of these phytoplanktonic inhabitants are intensely pigmented as are the semiplanktonic swimmers, e.g. the dark green acoel *Convoluta convoluta* (symbiotic algal cells; Ax and Apelt 1965, Dörjes 1968, Apelt 1969), the red pigmented *Macrostomum rubrocinctum* Ax, the reddish-brown proseriat *Monocelis fusca* Oersted, the black pigmented prolecithophoran *Enterostomula graffi* (De Beauchamp), and others (e.g. Westblad 1955, 1956). In the benthic/planktonic life-style gradient, phytoplanktonic species join the semiplanktonic *Promesostoma* species and the range leans more towards the planktonic. Thus, there are plathelminth species which usually live in the sediment, and there are species which do not usually touch the sediment. Presumably, disturbance events such as storm tides prevent these species from being restricted to either side, at least in shallow waters.

#### Plathelminth swimming and intertidal sand

Most of the plathelminth species studied are not restricted to intertidal sandflats. They also occur further up the tidal gradient – up to supralittoral beaches and salt marshes (Armonies 1987, Armonies and Hellwig-Armonies 1987, Hellwig 1987). In supralittoral salt marshes, many Plathelminthes are capable of encystment and are thus able to withstand intermittent environmental harshness (Armonies 1986a). Possibly some species from the sandflat studied have the same capability. Consequently, swimming would not be necessary were the environment to deteriorate. Many of the swimmers also occur in salt marsh creeks and salt

marsh pools filled by storm tides (Hellwig-Armonies and Armonies 1987). Such habitats often support a rich diatom flora and contain high numbers of copepods. But variations of environmental factors (salinity, temperature, oxygen availability) are generally stronger than on the tidal flats. Species living in the supralittoral have to tolerate wider ranges in physical factors and should be less influenced by such changes. This is the case in *Promesostoma caligulatum* (oxygen, light exposure, salinity), *P. marmoratum* (light, oxygen), *Pogaina kinnei* (oxygen), and *P. succica* (oxygen, salinity; Armonies 1988c). Swimming in the water column might therefore be part of an opportunistic life-style.

Since many of the swimming Plathelminth species also occupy habitats other than the studied intertidal sandflat, active swimming in the water column is not a local phenomenon. Even some brackish water Plathelminthes of supralittoral salt marshes entered an experimental water column (Armonies unpublished data), although these locations were only flooded during storm tides. Presumably they enter the water column for dispersal across the marshes. Most of the species studied are not restricted to the Wadden Sea but occur over wide geographical ranges, e.g. in the Baltic Sea (Karling 1974, Armonies 1988d), the Mediterranean Sea (Ax 1956) and on the eastern side of the Atlantic Ocean (Ax and Armonies 1987). Thus, plathelminth emersion from the sediment may be expected anywhere.

## Conclusions

The traditional tripartition of Plathelminthes into benthic, phytal dwelling, and planktonic species needs to be revised. 'Benthic' species include life-styles which are continuously changing from benthic to semiplanktonic, with phytal fauna joining the semiplanktonic side of the spectrum. Possibly the gradient continues further to include planktonic species. Among the traditionally viewed 'benthic' species, intensity of body pigmentation, feeding type, and depth in the sediment occupied during low tide may be used as estimators of the specific swimming activity.

Swimming in the water column allows for dispersal by currents and thus a change of locality without much energy expenditure. Swimmers may escape from unfavourable factors in the sediment, or exploit additional resources, either after returning to the sediment (? diatom-feeders), or in the water column. Therefore strict correlations between swimmer abundance and some sediment properties cannot be expected, even if the respective species really do respond to these properties (e.g. by a shortened period of stay in the respective sediment). Likewise, it should be stressed that evaluations of the taxonomic composition and counts of abundance can only yield a snap-shot which might be strongly changed the tide after. Such short-term changes may affect descriptive as well as experimental studies. Since many of the species involved are not restricted to the studied habitats, or to the Wadden Sea, further generalization of these observations is assumed.

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