The importance of turbellarians in the marine meiobenthos: a review

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Abstract

Recent data and opinions on meiofaunal ecology are briefly reviewed; and from scattered data, the place of turbellarians in the meiobenthic community is discussed. Turbellarian diversity, density, and biomass are higher in sandy habitats than in muddy bottoms. In sand, turbellarian diversity is of the same magnitude as that of other important meiofaunal taxa, while densities range between 7–25% of the total meiofauna. Mean individual turbellarian dry weight seems to be four times that of nematodes and in sandy habitats turbellarian biomass may be equal to or excede that of nematodes. Most turbellarian species may be considered as predators and in this respect may take the place occupied by macrofaunal species in muddy sediments. mens.

Introduction

Ecological studies on the meiofauna have expanded considerably during the last 20–25 years. Much attention has been focused on nematodes and harpacticoids which are often considered the dominating meiofaunal representatives. The soft-bodied fauna is proportionally disregarded because most soft-bodied animals must be studied alive and/or with light histological techniques in order to be identified. Turbellarian ecology has been dealt with in some autoecological studies (Ax, 1951, 1956, 1959; Ax & Ax, 1970; Dörjes, 1968; Ehlers, 1973; Faubel, 1976; Schmidt, 1972a, b; Sopott, 1973) and less in a more general perspective (Bilio, 1964, 1967; Ax, 1969, 1977; Pawlak, 1969; Gray & Rieger, 1971; Boaden, 1981; Purschke, 1981; Riese, 1984; Xylander & Reise, 1984).

In the present paper we attempt to determine a possible role of the Turbellaria within the meiobenthic community in terms of species-diversity, density, biomass, place in the trophic chain. Our speculations are based on the scattered (qualitative and quantitative) data that could be found in the literature on meiofauna and in some of our own preliminary observations.

Turbellarians as members of the meiobenthos

The term 'meiobenthos' (meiofauna) was introduced by Mare (1942) to indicate those benthic metazoans smaller than the 'macrobenthos' but larger than the 'microbenthos'. In practice the meiofauna consists of animals which pass through a 0.5–2 mm sieve but are retained on a sieve of 0.1–0.04 mm mesh width (McIntyre, 1969; Coull & Bell, 1979; Platt, 1981). However, many turbellarian species are larger than 2 mm (even up to more than 1 cm) and are nevertheless considered meiofaunal elements.

In a recent study, Warwick (1984) compared life strategies of several taxa in different marine benthic communities and concluded that animals larger than ±45 μg dry weight (macrofauna) have a planktonic development, disperse in the larval

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stage, have a continuous growth throughout life with a generation time of more than one year, and feed in indiscriminate fashion on particles (but often selected on the basis of particle size). Species smaller than ±45 μg dry weight (meiofauna) have no planktonic development, disperse in the adult stage, have an asymptotic growth to a maximum body size with a generation time of less than one year, and feed by selection on size but also on shape or quality of the particles.

From these observations, meio- and macrofauna can be redefined on the basis of biological criteria *and* of body size. Except for some triclads and polyclads all marine benthic turbellarians fit very well into this new definition, and some of them must be considered 'large meiobenthos'.

Two factors – among others – characterize the benthic habitat: grain size of the sediment and water movement (dynamism); and these are related to each other to some extent.

Grain size and packing of the grains determine the space available between grains for the so called *interstitial meiofauna* (Coull & Bell, 1979). The coarser the sand, the larger the interstices and vice versa. In a very fine sediment, such as mud, animals move by displacement of the sediment and so constitute *burrowing meiofauna.* Intertidal animals are small and/or elongate and exhibit a number of adaptive features (Remane, 1933; Wilson, 1935; Swedmark, 1964); there seems to be a relation between body shape and grain size (Wieser, 1959), but there is, of course, a limit: in mud-living meiofauna body size and shape are not related to grain size (Coull & Bell, 1979).

Sandy bottoms, especially on beaches exposed to wave action, are mostly dynamic environments. Muddy bottoms, found in estuaries, lagoons, saltmarshes and sublittoral places, are much less dynamic. Turbellarians are not very abundant in muddy bottoms: we find a lower diversity, as in other meiofauna taxa, and a lower density, contrary to many other meiofaunal taxa (see below).

In a sandy habitat, both diversity and density of turbellarian species are high (see also below) and all orders are represented. They often share a number of characteristics: they are haptic and may be quite contractile or move fast by muscular action, some of them have a tail appendage, many have long sensory bristles, a chordoid structure can be present, and some are extremely elongate. All these characteristics are considered adaptations to the interstitial way of life or to the dynamism of the environment or to both (Remane, 1933; Hyman, 1951; Ax, 1963, 1966; Boaden, 1968; Bush, 1968). The functional significance of these features has been discussed by Ax (1963, 1966) and Bush (1968). Some of these characteristics, such as adhesive papillae, sensory bristles, and body musculature, are well developed in Otoplanidae which is the dominating metazoan group in the swash zone, the most dynamic zone of the beach and called the Otoplana zone by Remane (1933).

As with other interstitial meiofaunal groups, there seems to be a relation between grain size of the sand and body length of the turbellarians. On the beaches of the island of Sylt (Germany) with coarse sand (400–500 μm; Schmidt, 1968) Proseriata is the dominating group, with many representatives of the Monocelididae, Coelogynoporidae, and Nematoplanidae reaching up to more than 1 cm in length (Sopott, 1973; Noldt & Wehrenberg, 1984). On the other hand at Robin Hood's Bay in fine sand (Gray & Rieger, 1971) and at the Belgian coast also in fine sand (Martens, 1984) Neorhabdocoela up to ±2 mm (Dalyellioida and Kalyptorhynchia, respectively) dominate the turbellarian fauna (together with the Acoela). According to Douglas (1984), there might be a relation between body size and grain size in the acoel *Convoluta roscoffensis.*

Diversity

The diversity in the marine meiofauna is generally high, and the discovery of new species (and even higher taxa) goes on even in intensively investigated areas. Sandy bottoms (especially fine and medium sand) contain more meiofaunal species than does mud (especially in brackish water) (Platt & Warwick, 1980; Remane & Schlieper, 1971).

Ecological studies on meiofauna, have paid most attention to the so-called 'hard-bodied' meiofauna such as nematodes (see Gerlach, 1980) and harpacticoids; the 'soft-bodied' meiofauna, to which the turbellarians belong, is mostly neglected. The reason is obvious: turbellarians must be extracted from the sediment and studied alive as soon as possible after sampling. This is also the main reason why sublittoral turbellarians are relatively poorly known. Moreover, taxonomists working with marine turbellarians are few. They are often compelled to focus their attention on some orders and to disregard others. Most areas have been investigated only over a short period of time. Finally, it is known that the methods used to extract turbellarians are far from being 100% efficient (Martens, 1984) and are almost of no use at all in a muddy sediment. For all or some of these reasons, the numbers of turbellarian species occurring in a given area are undoubtedly underestimated, and lists of species are necessarily incomplete, especially in muddy sediments. In mud, generally the most fragile turbellarians such as acoels and some smaller species of Macrostomida, Dalyellioida, and Monocelididae form the majority (own obs., see also Karling, 1974; Riedl, 1956; Steinböck & Reisinger, 1930): they are often damaged during extraction or simply lost or overlooked.

Nevertheless, when the data on turbellarian diversity (Table 1) are compared with the diversity of the much better investigated nematodes (Platt & Warwick, 1980: 735, Table III), it is obvious that in many instances numbers of turbellarian species are of about the same magnitude as those for nematodes. For the whole North Sea, 735 species of nematodes and 515 of harpacticoids are known (Heip *et al.*, 1983). A survey of the literature shows that over 400 turbellarian species are known from the same area but almost exclusively from littoral stations. Considering the data on the German Wadden Sea, where nematodes and harpacticoids as well as turbellarians have been investigated intensively, the following figures emerge: there are about 300 turbellarian, 300 nematode, and 150 harpacticoid species reported here (Wolff & Dankers, 1983). And for the island of Sylt: 230 turbellarian (Wehrenberg, 1983) and 178 nematode (Blome, 1982, 1983) species are reported.

To conclude we can safely state that species diversity of turbellarians in the meiofauna is at least similar to that of nematodes and may perhaps even be higher than that of harpacticoids, at least in some marine sandy habitats. Species diversity of turbellarians in mud is considerably lower than in sand, but as stated above, this is also valid for many other meiofaunal taxa.

Densities

The densities of the total meiofauna vary according to kind of sediment, latitude, depth, salinity, wave action, etc. On the average, one can expect to find 1000–2000 individuals 10 cm^{-2} (Coull & Bell, 1979). Densities tend to increase in detritus-rich muddy sediments with the highest values in intertidal mudflats of estuaries, lagoons, or salt-marshes. Densities are intermediate in muddy or silty sands and lowest in clean sand, especially on very exposed sites. There is also a decrease in meiofaunal density with depth into the ocean (Coull & Bell, 1979).

Table 1. Numbers of species of Turbellaria known from various localities.

Number of species	Location	Authors
111	Baltic Sea, Sandy habitats	Karling, 1974
56	Baltic Sea, Muddy habitats	Karling, 1974
302	German Wadden Sea*	Wolff & Dankers, 1983
230	Island of Sylt, Germany	Wehrenberg, 1983
60	Sylt, Sublittoral	Wehrenberg, 1983
39	Netherlands Delta area, Sublittoral	Martens & Schockaert, 1981
91	Netherlands Delta area, Salt-Marsh	Den Hartog, 1977
110	Belgian coast, Littoral	Own observations
200	Bay of Calvi, Corsica, Sandy habitats	Own observations
56	Bay of Calvi, Corsica, Periphyton	Own observations
70	Romanian Littoral waters	Mack-Fira, 1974
78	Kieler Bucht, Germany	Ax, 1951
45	Coastal lakes of French Mediterranean*	Ax, 1956
72	Ponto-Caspian brackish water*	Ax, 1959

* Some species of the periphyton included.

Table 2. Some maximum meiofaunal densities for various detritus-rich and muddy sediments.

Habitat	Locality	Max. Density	Authors
Estuary	Lynher Estuary, England	22×10^6 ind.m^{-2}	Warwick & Price, 1979
Estuary	Westerschelde Estuary, Belgium	17×10^6 ind.m^{-2}	Van Damme *et al.*, 1980
Lagoon	Bay of Arcachon, France	12×10^6 ind.m^{-2}	Lasserre *et al.*, 1975
Salt-marsh	Georgia, USA	16×10^6 ind.m^{-2}	Teal & Wieser, 1966
Salt-marsh	Rhode Island, USA	10×10^6 ind.m^{-2}	Nixon & Oviatt, 1973

In mudflats, maximum total meiofauna densities may reach ten times the average (Table 2) and nematodes may account for more than 90% of the total meiofaunal density (Bilio, 1966; Coull & Bell, 1979; Elmgren, 1976; Heip *et al.*, 1982; Platt & Warwick, 1980; Skoolmun & Gerlach, 1971; Warwick, 1971).

Turbellarians may occur in densities of 100–500 individuals 10 cm^{-2} and may represent between 7–25% of the meiofauna in sandy bottoms and even more in some particular places (Table 3). In muddy systems, however, turbellarians constitute only a few percent of the total meiofauna (McIntyre, 1969; Straarup, 1970; Watzin, 1983). From our own experience with muddy sediments, in both littoral and sublittoral stations in the Mediterranean (Calvi, Corsica) and in the North Sea, we can confirm that they are poor in turbellarians (but see above).

On the other hand, some data are known from sites showing extremely high (absolute or relative) densities of turbellarians (Table 4; all the species here are rather large, 1.35–7 mm long). The well-known Otoplana zone is another example.

Concerning densities of turbellarians in the meiofauna, we can conclude that in sandy habitats they may constitute from 7 to 25% of the total meiofauna but are much less abundant in mud. In some restricted areas they may become the dominant metazoan group.

Table 3. Comparison of meiofaunal and turbellarian densities in various localities.

Individuals 10 cm^{-2}		% of the total meiofauna	Habitat	Locality	Authors
Meiofauna	Turbellarians				
38– 655	27–591	28 –95	Exposed beaches	Spitsbergen	Radziejewska & Stankowska-Radziun, 1979
67–4092	3–101	1 –10	Sheltered, detritus-rich beaches	Spitsbergen	Radziejewska & Stankowska-Radziun, 1979
523–2828	96–273	10 –22	Steep Northern beach	Firemore, Scotland	McIntyre & Murison, 1973
833–4284	124–306	5 –21	Less steep Southern beach	Firemore, Scotland	McIntyre & Murison, 1973
2466–4415	60–389	2 –13	Sublittoral	Firemore, Scotland	McIntyre & Murison, 1973
51– 230	4– 37	4 –31	Exposed beach	Robin Hood's Bay, England	Gray & Rieger, 1971
420–3815	10– 48	0.3– 8	Estuary	Porto-Novo, India	McIntyre, 1968
603	245	41	Sandy beach	Porto-Novo, India	McIntyre, 1968
1125	37	3	Muddy beach	Porto-Novo, India	McIntyre, 1968
741–4904	24–408	2 – 9	Muddy-sand beach	Dalnezelenetsky Bay, Barents Sea	Galtsova & Platonova, 1980
80– 375	–	5 –15	Sheltered coarse-sand beaches	Sylt, Germany	Schmidt, 1968
3152	236	7.5	Sand flat	Sylt, Germany	Reise, 1983c
454–4682	54–407	7 –24	Meidum-exposed sandy beaches	Belgian coast	Own observations

Table 4. Turbellarian species showing high (absolute or relative) densities.

Species	Locality	Max. Density	Authors
Paromalostomum coronum	Reid State Park, USA High-energy beach	dominating metazoan species	Spurr, 1983
Paromalostomum fusculum	Island of Sylt, Germany	115 500 ind. m^{-2}	Pawlak, 1969
Paromalostomum fusculum	Belgian Coast	61 000 ind. m^{-2}	Martens, 1984
Pseudomonocelis ophiocephala	Black Sea, Russia	115 800 ind. m^{-2}	Murina, 1981
Pseudomonocelis ophiocephala	Protected sand beaches, Corsica and Italy	dominating metazoan species	Own obs.
Triporoplana synsiphonioides	Protected gravel beaches, Corsica	dominating metazoan species	Own obs.

Biomass

On the average, the biomass of meiobenthos is between 1 and 2 g dwt (dry weight) m^{-2} (Coull & Bell, 1979). In areas with high densities, it may rise to 4.9 g dwt m^{-2} (Van Damme *et al.*, 1980).

Mean individual dry weight of nematodes in the meiofauna averages between 0.15 and 0.45 μg (Wieser, 1960; Juario 1975; McLachlan, 1977; McIntyre, 1978; Heip *et al.*, 1982) and the individual dry weight of turbellarians appears to be about four times that of nematodes (Table 5). We have seen (Table 3) that in sandy habitats turbellarians may represent 7–25% of total meiofauna density, and can conclude in light of this 4:1 ratio in dry weight that turbellarian biomass may thus be equal to or exceed that of nematodes in some instances. Nematodes often constitute much less than half of the total meiofauna biomass in sandy habitats (Guille & Soyer, 1969; McIntyre & Eleftheriou, 1968; McIntyre & Murison, 1973; McLachlan, 1977; Platt & Warwick, 1980), and so it is clear that in those systems turbellarians may be relatively more important in terms of biomass.

Table 5. Average individual dry-weight biomass for turbellarians.

Author	Size classes in mm	μg dwt/ind.
Ankar & Elmgren, 1976	/	1.4
Coull, 1970	/	2
Van Damme & Heip, 1977	/	2.4
Faubel, 1982	0.5–1.0	0.63
Faubel, 1982	1.5–2.5	1.73
Faubel, 1982	3.0–4.0	8.81

Place in the food web

Turbellarians with a pharynx simplex or a pharynx doliiformis may swallow relatively large food particles. Those with a pharynx rosulatus or a pharynx plicatus can also swallow particles or suck out a prey even larger than themselves (see Straarup, 1970 with references). Thus, on the whole, turbellarians feed on a variety of food items.

Food requirements of turbellarians may be known by direct observations, feeding-experiments (e.g. in culture), or by the analysis of gut contents. According to Straarup (1970) and Reise (1983a, b) the diet of many acoels and dalyellioids consists mainly of diatoms, but the majority of turbellarians appear to be predators. Turbellarians are known to eat ciliates, hydroids, nematodes, turbellarians, copepods, amphipods, annelids, and also dead animals (Bilio, 1967; Elmgren, 1976; Hyman, 1951; Jennings, 1957, 1974, 1977; Karling, 1974; Murina, 1981; Pawlak, 1969; Reise, 1983a, b; Remane, 1933; Spurr, 1983; Watzin, 1983; Westblad, 1923; own observations). In cultures they can be kept alive with tubificids, *Artemia* nauplii, copepods, or meat (Curini-Galletti, Riser, pers. commun.; Spurr, 1983).

Prey consumption may be considerable. A population of *Pseudomonocelis ophiocephala* with a mean annual density of 14 640 individuals m^{-2} may consume about 589 000 amphipods (*Gammarus insensibilis*) a year (Murina, 1981). Watzin (1983) tested the predation of turbellarians on settling macrofauna larvae and juveniles. She found that increased densities of turbellarians significantly reduce densities of juvenile spionids and some other deposit feeders.

For the time being there is no strong evidence that turbellarians feed on bacteria. Reise (1983a, b) considered some species to do so, but his conclusion was based on the absence of any recognisable material in gut contents (pers. comm.). Straarup (1970) considered the bacteria found in some species to be engulfed along with the prey or even as food of the prey animals themselves. Contrary to some statements (Jennings, 1977), we have found no evidence that turbellarians feed on detritus.

From the data now available we conclude that bacteria and detritus play a minor role (if any at all) in turbellarian diet, that some turbellarians prefer diatoms, and that the majority of them are mainly predators or scavengers. This implies that they belong to a high trophic level (McIntyre & Murison, 1973; Straarup, 1970) and exert predation pressure on the rest of the meiofauna and on small animals of the macrofauna.

Is there predation on turbellarians? Turbellarians are known to be eaten by other turbellarians (see above); some polychaetes, like *Nereis diversicolor* and some macrofauna deposit feeders seem to eat turbellarians (Bilio, 1967; Straarup, 1970; Watzin, 1983), but it is generally accepted that there is no heavy predation on turbellarians because of their defensive use of rhabdites and kleptocnids (Hyman, 1951; Karling, 1966). It is, however, evident that turbellarians would not be easy to identify in the gut contents of possible predators.

Possible role of turbellarians in the meiofauna

Much attention has been paid to the role of the meiofauna in an ecosystem, and much research has been carried out to establish the trophic relations between meio- and macrofauna. From an extensive review of the literature on this subject, Coull & Bell (1979 with many references) suggested that 'the mud/detrital meiofauna [may]... serve as a significant source of food for higher trophic levels... [meaning macrofaunal predators including fishes and natant crustaceans], whereas in sandy substrates the members of the meiofauna serve primarily as relatively rapid metazoan nutrient regenerators.' In other words, in a muddy bottom a significant portion of the biomass production realised in the meiofauna [with a production rate at least five times that of the macrofauna (Gerlach, 1971)] is transferred to the macrofauna, whereas biomass transfer is much less significant in a sandy substrate.

In a sandy habitat, especially clean sand of an exposed beach, macrofauna density is relatively low because the life strategies of the animals do not fit very well into such a disturbed environment (Gerlach, 1971; McIntyre, 1968, 1978; Renaud-Debyser & Salvat, 1963; Warwick, 1981, 1984; Whitlatch, 1980). The 'high trophic levels' (predators, secondary predators, etc.) are to be found within the meiofauna itself.

We have concluded in previous sections that diversity, density, and biomass of turbellarians may become rather important in sandy habitats and that many turbellarians (especially the larger ones) are most probably voracious predators. We may assume that in sandy habitats these turbellarians belong to the 'higher trophic levels,' the end of the trophic chain. Also, among nematodes e.g. more predators are found in sandy than in muddy bottoms (Platt & Warwick, 1980).

As Coull & Bell (1979) state, '... it is becoming increasingly apparent that [apart from physical properties of the habitat] biological interactions ... [such as] predatory controls play a ... role in structuring meiofaunal assemblages...' Perhaps we have here an example of how a low predatory pressure from the macrofauna induces an increase in meiofaunal predators. However, one can wonder whether those meiofaunal predators themselves control the macrofaunal assemblages, as a result of either food competition or predation from the meiofauna on young members of the macrofauna (Watzin, 1983).

Conclusions

Our ideas about the importance of turbellarians in the meiobenthic community can be summarized as follows:

1. Concerning their life strategies and body size ($< 45\ \mu g$ dwt), turbellarians certainly belong to the meiofauna. They are well adapted to the interstitial way of life in sandy (dynamic) habitats.
2. Diversity, density, and biomass of turbellarians are higher in such habitats than in muddy bottoms. In sand, the diversity of turbellarians can be of the same magnitude as that of nematodes, and turbellarian biomass can be even higher.

3. The majority of turbellarian species must be considered to be predators and thus to represent the higher trophic levels of the trophic chain, at least in sandy bottoms where they may take the place of the macrofaunal predators of a muddy substratum.

Our main aim with this paper is to attract the attention of meiofaunal ecologists to a component too much neglected in the study of meiofaunal assemblages. Much remains to be investigated in turbellarian ecology, in the field as well as in laboratory experiments: diversity and density in habitats with different dynamism, respiration and reproduction rates, feeding and food requirements, competition, etc. But it is clear that turbellarians must be taken into consideration when assessing any of the parameters of the ecosystem.

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