# DISTRIBUTION OF MARENZELLERIA VIRIDIS (POLYCHAETA: SPIONIDAE) IN THE SOUTHWESTERN BALTIC SEA IN 1993/94 - TEN YEARS AFTER INTRODUCTION

Jan Kube, Michael L. Zettler, Fritz Gosselck, Susanne Ossig & Martin Powilleit

SARSIA

Kube, Jan, Michael L. Zettler, Fritz Gosselck, Susanne Ossig & Martin Powilleit 1996 07 01. Distribution of *Marenzelleria viridis* (Polychaeta: Spionidae) in the southwestern Baltic Sea in 1993/94 - ten years after introduction. – *Sarsia* 81:131-142. Bergen. ISSN 0036-4827.

*Marenzelleria viridis* (Verrill, 1873), a North American spionid polychaete, was first recorded in brackish water ecosystems of the Wadden Sea and Baltic Sea in the early 1980s. It has spread rapidly and is now a dominant element of the macrozoobenthos in meso- and oligohaline estuaries and coastal lagoons. The distribution and abundance of this polychaete was studied in the southwestern part of the Baltic Sea in 1993/94 in relation to environmental factors. All available macrozoobenthos samples from German Baltic waters were used to construct a general distribution map. Highest abundances and biomasses were found in semi-enclosed lagoons (39 000 ind. m$^{-2}$ and 70 g ash free dry weight m$^{-2}$). The western horizontal distribution border and the vertical distribution range were following the 15 ‰ isohaline. Neither a horizontal nor a vertical limit was found to the east. Dense settlement was restricted to sediments with an organic content of less than 5 % and a silt content of less than 10 %.

Simultaneous population studies were carried out in the Oder Estuary and the Darss-Zingst Bodden from April 1993 to April 1994. Three different age groups were identified throughout the year. Settlement of larvae took place in autumn. Successful larval settlement was restricted to areas with a salinity above 5 ‰ and a winter phytoplankton concentration above 5 g Chl *a* m$^{-3}$. Benthic stages were found to be highly motile. Adults occurred up to 50 km away from recruitment areas. Potentially important causes of dispersal processes are discussed.

*Jan Kube & Martin Powilleit, Institut für Ostseeforschung Warnemünde, Seestrasse 15, 18119 Rostock, Germany – Michael L. Zettler, Universität Rostock, Fachbereich Meeresbiologie, Freiligrathstrasse 7/8, 18051 Rostock, Germany – Fritz Gosselck, Institut für Angewandte Ökologie, Lindenweg 2, 18184 Neu Broderstorf, Germany – Susanne Ossig, Universität Greifswald, Zoologisches Institut, J.-S.-Bach-Strasse 11/12, 17489 Greifswald, Germany.*

Keywords: Polychaeta; *Marenzelleria viridis;* distribution; population dynamics; Baltic Sea.

## INTRODUCTION

The introduction of alien species to marine areas is an old phenomenon. Recently, unintentional introductions of coastal marine species to new environments have increased. Extensive man-induced changes of estuaries and the increasing size and speed of ships have augmented the risk of spreading species over seas. Ballast water and artificial waterways have been described to be the main causes of unintentional introductions (Carlton 1985; Jansson 1994).

The Baltic Sea is especially receptive to successful invadings. The history of coastal lagoons is short (2 000-6 000 years) and species assemblages have a low diversity. Many niches are unsaturated. About 30 animal species have been reported as introduced east of the Arkona Basin until 1984 (Leppäkoski 1984). Among these, two macrobenthic bivalve species, *Dreissena polymorpha* (Pallas) and *Mya arenaria* (L.), make up the predominant biomass in some coastal areas (Leppäkoski 1991).

A North American polychaete, *Marenzelleria viridis* (Verrill, 1873), was introduced to the Baltic during the 1980s. The first specimens in Europe were found in 1982 in the Forth Estuary, Scotland (McLusky & al. 1993) and in 1983 in the Ems estuary between The Netherlands and Germany (Essink & Kleef 1988). It is assumed that larvae were transported across the Atlantic in the ballast water of ships. Since, it has spread rapidly around the North Sea (Essink & Kleef 1993).

Bick & Burckhardt (1989) observed the first specimens of *M. viridis* in the Darss-Zingst Bodden, a coastal lagoon system of the southern Baltic Sea, in 1985. Densities of about 1 000 individuals m$^{-2}$ were reported from the eastern part of the Darss-Zingst Bodden and all over the Oder Estuary already in 1988 (Gruszka 1991a; Arndt

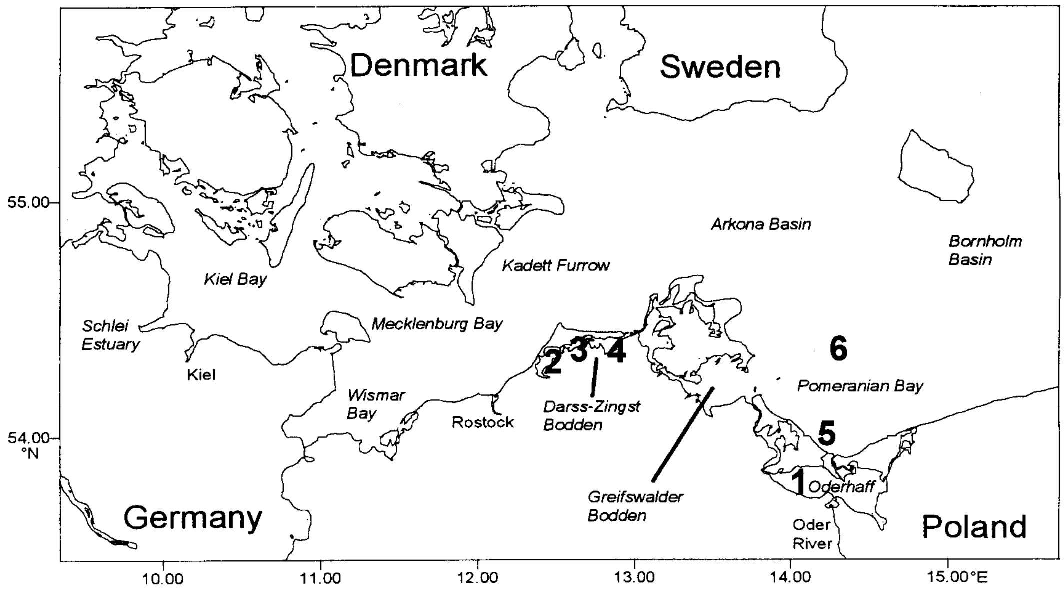

Fig. 1: Study area in the Baltic Sea. Labels indicate subareas mentioned in the text.

1994; M. Saavedra pers. commn). This spionid polychaete was probably imported by ballast water to one of the big harbours in the Oder Estuary around 1983/84. The polychaete dispersed eastward to Estonian inshore areas and to the south coasts of Sweden and Finland. The first specimens were found there in 1989 and in 1990 (Persson 1990; Norkko & al. 1993; Zmudzinski & al. 1993). Today it is dominant in some Baltic coastal benthic communities at about 90 % (e.g. Zmudzinski 1993; Zettler 1994). West of the Oder Estuary it was reported only for the Wismar Bay by Prena & Gosselck (1989) and the Schlei Estuary (V. Schrören, pers. commn). The North Sea and Baltic Sea populations are of different genetic origin (Bastrop & al. 1995). There is no doubt, that these populations were introduced separately. They might even belong to different species (R. Bastrop & M. Röhner, pers. commn).

*M. viridis* has been studied intensively since it was discovered to become an important component of the coastal macrozoobenthos of the Baltic Sea. Field studies and laboratory investigations were carried out to analyse the life cycle (Bochert & al. 1993), the distribution and physiological capacities according to ecological factors (Zmudzinski & al. 1993; Bochert & Bick 1995; Fritzsche & von Oertzen 1995; Zettler & al. 1995). This paper presents a descriptive picture of the recent distribution of *M. viridis* for the southwestern Baltic Sea. Comparable analyses of population dynamics were used simultaneously in several subareas of the Oder Estuary and the Darss-Zingst Bodden to describe its niche in the field in relation to various environmental factors.

## MATERIAL AND METHODS

### *Study area*

Samples were collected in 1993/94 from the German part of the Baltic Sea and adjacent Polish waters (Fig. 1). The salinity ranged from 15-25 ‰ in the West (Kiel Bay) to less than 2 ‰ in the East (Oderhaff). Samples were taken in shallow coastal regions up to 0.5 m depth and down to 40 m deep offshore (Arkona Basin). A recent description of the hydrography of the southwestern part of the Baltic Sea is given by Nehring & al. (1994). Detailed hydrographic data are presented for the Oder Estuary and the Darss-Zingst Bodden by Lampe (1993) and Schlungbaum & al. (1994a, b).

### *Sampling design and data analysis*

Macrozoobenthos samples were collected in the Darss-Zingst Bodden (50 sampling sites), the Pomeranian Bay (35 sampling sites) and the Oderhaff (85 sampling sites) between April and September 1993 to compute detailed distribution maps. Density isolines were calculated by kriging with WINSURF software package.

The applied sampling methods were comparable for these areas. Reineck-Box corers (0.0225 m$^2$ and 0.006 m$^2$, penetration depth 15-20 cm) were used in the Pomeranian Bay and in the Oderhaff. Sampling was carried out by a hand-operated tube corer (0.0078 m$^2$, penetration depth 40 cm) in the Darss-Zingst Bodden. All samples were sieved with a 0.5 mm sieve. Ash free dry weight (AFDW) was measured following the HELCOM-guidelines (Helcom 1988) for samples collected in the Pomeranian Bay.

*M. viridis* is known to burrow up to 35 cm deep into the sediment. Only about 20-30 % of the large mature worms live in the upper 10 cm of the sediment. In the Darss-Zingst Bodden, occasionally, up to 45 % of the adults were found burrowed deeper than 20 cm (Zettler & al. 1994). However, the penetration depth of the box corer was deep enough to catch all worms in the Pomeranian Bay (burying deeper than about 10 cm was prevented there by a thick layer of bivalve shells). Perhaps, 10-20 % of the worms were lost in samples from the Oderhaff. Unfortunately, an intercalibration with the deep penetrating hand-operated tube corer was technically impossible.

Detailed population studies were carried out in selected subareas between April 1993 and April 1994 at 1-3 sites (Fig. 1, not for subarea 4). Sites of subarea 1 were 2-4 m deep. Sites of subareas 2 and 3 were 0.5 m deep. Sites of subareas 5 and 6 were 9-10 m deep. All samples taken from these areas were collected in the same way as described above. Maximum width of all specimens was measured within the first 30 segments by only two persons to minimize systematic errors.

We also analyzed sediment parameter and phytoplankton concentration in all subareas. According to the small-scale spatial variability in the distribution of *M. viridis* (Zettler & Bick 1996), relationships between sediment parameter and densitiy estimates were plotted only for macrofauna and sediment samples, simultaneously collected. Sediment samples were taken from the upper 5 cm. Median grain size, silt content (relative DW of the fraction < 63 µm after wet sieving) and organic content (loss on ignition after incineration at 500° C) were measured. Samples taken before April and later than September were excluded from the analysis to minimize the impact of reproductive processes. Monthly measurements of water chlorophyll *a* concentration were obtained from 1-5 sites per subarea between 1992 and 1994. Chlorophyll *a* was analysed according to Jeffrey & Humphrey (1975). Data were splitted into summer months (June-September) and winter months (November-February). Spring bloom data from March-May and data from October (maximum of planktonic larvae) were excluded.

Salinity was measured for each sampling site and date.

Furthermore, we computed a distribution map for the German part of the Baltic Sea. Several hundred macrozoobenthos samples were collected in this area in 1993/94, mainly for monitoring purposes. A large variety of sampling gear was applied due to the different scope of each investigation. The sampling methods applied in the Oder Estuary and in the Darss-Zingst Bodden were already described. An Ekman-Birge grab sampler (0.021 m$^2$, penetration depth 5-10 cm) was used in a few coastal inlets in the West. Van-Veen grab samples (0.1 m$^2$, penetration depth 8-12 cm) were taken in Kiel Bay, Mecklenburg Bay, Wismar Bay, and in the Arkona Basin. Al these samples were sieved with a 1 mm sieve (Table 1).

Hence, large differences in density estimates occurred according to the penetration depth of the grabs applied. A logarithmic scaling of density isolines was used, therefore, to compute a general distribution map. Density estimates obtained from Ekman-Birge grab samples for instance, presented only between 30 % and 50 % of the true values. An intercalibration between box corer samples, sieved with a 0.5 mm sieve, and Van Veen grab samples, sieved with a 1 mm sieve, was performed in the Pomeranian Bay in April and October 1993. Mean densities of *M. viridis* were about 50 % lower in Van Veen grab samples than in box corer samples (Powilleit & al. 1996). However, the impact of underestimation of densities onto the shape of density isolines was less important, since most of the grab samples were taken in the West, where no *M. viridis* occurred.

Tab. 1: Sampling methods, applied in different parts of the study area.

| subarea | grab type | sampling area (m$^2$) | penetration depth (cm) | sieve mesh size (mm) |
|---|---|---|---|---|
| Kiel Bay | Van Veen | 0.1 | 10-12 | 1 |
| Wismar Bay | Van Veen | 0.1 | 8-10 | 1 |
|  | Ekman Birge | 0.021 | 5-10 | 1 |
| Mecklenburg Bay | Van Veen | 0.1 | 10-12 | 1 |
| Warnow Estuary | Van Veen | 0.1 | 8-10 | 1 |
|  | Ekman Birge | 0.021 | 5-10 | 1 |
| Arkona Basin | Van Veen | 0.1 | 10-12 | 1 |
| Darß-Zingst Bodden | hand-operated tube corer | 0.0078 | 40 | 0.5 |
| Greifswalder Bodden | box corer | 0.006 | 15-20 | 0.5 |
| Pomeranian Bay | box corer | 0.0225 | 15-20 | 0.5 |
| Oderhaff | box corer | 0.006 | 15-20 | 0.5 |

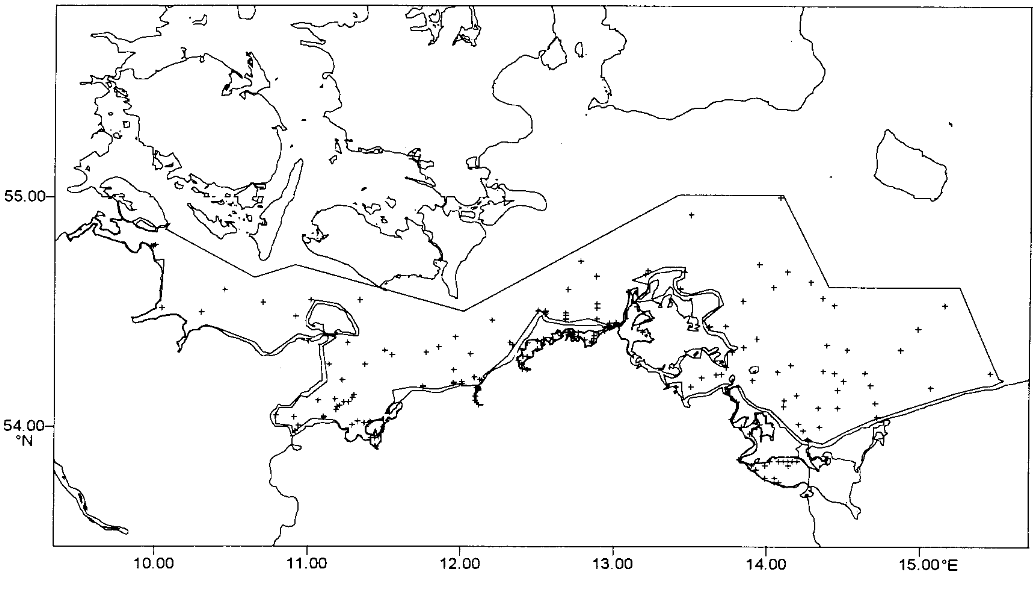

Fig. 2: Distribution of sampling sites used for plotting a distribution map.

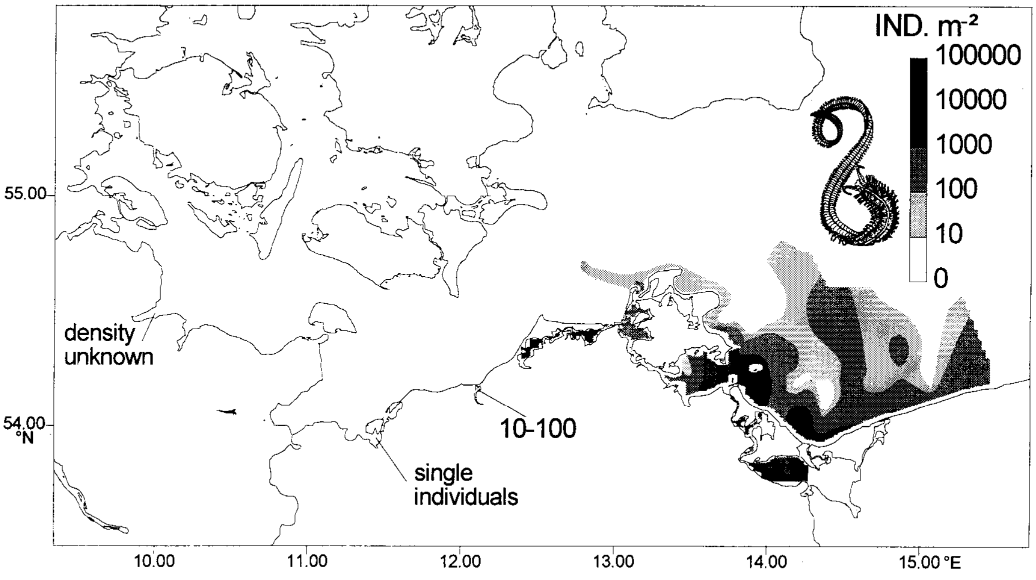

Fig. 3: Distribution and densities of *Marenzelleria viridis* in the southwestern Baltic Sea in 1993/1994.

Differences in density estimates were caused also by differences in the sieve mesh sizes. Juveniles were observed passing completely through the meshes of the 1 mm sieve up to a size of less than 0.8 mm (Powilleit & al. 1996). Settlement of larvae takes place in the Darss-Zingst Bodden between October and January (Bochert & al. 1993). Juveniles from inner coastal lagoons reach a width of about 1 mm in March/April. Therefore, samples collected between October and March were excluded from the data analyses to minimize the impact of juvenile abundances. At least 200 samples could be used for computing a general distribution map with WINSURF software package (Fig. 2).

## RESULTS

### *General distribution in the southwestern Baltic*

*M. viridis* was found in all inner coastal waters east of Mecklenburg Bay (Fig. 3). Mean densities ranged between 1 000 and 5 000 ind. m$^{-2}$. Maximum values were 39 000 ind. m$^{-2}$ for the Darss-Zingst Bodden in May 1994 and 28 000 ind. m$^{-2}$ for the Oderhaff in summer 1993. Much lower densities were observed in offshore waters. Densities in the Pomeranian Bay decreased rapidly about 5 miles off the Greifswalder Bodden from 3 000 to 4 000 ind. m$^{-2}$ to 100-300 ind. m$^{-2}$. Densities at the southern slope of the Arkona Basin did not exceed 30 ind. m$^{-2}$ at 30 m water depth. No specimens were found in the deeper central part of the Arkona Basin. Low densities between 10 and 30 ind. m$^{-2}$ were found at 30 m depth in the eastern part of the Kadett Furrow. The polychaete was not found in Mecklenburg Bay. Only single individuals occurred occasionally north of the Warnow Estuary near Rostock. Within this estuary densities ranged between 10 and 100 ind. m$^{-2}$. A single specimen was collected during extensive sampling in the innermost part of the Wismar Bay in 1993. No worms were found in Kiel Bay. The species was reported recently from the Schlei Estuary which enters Kiel Bay. Densities seem to be high there, but have not yet been estimated (V. Schrören, pers. commn). These animals also belong to the Baltic Sea genotype of *M. viridis* (R. Bastrop & M. Röhner, pers. commn).

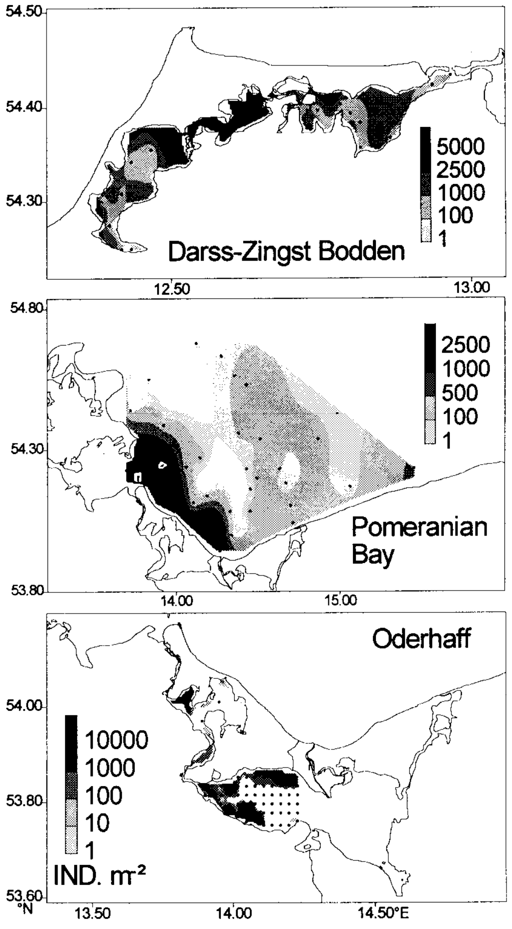

Fig. 4: Distribution and densities of *Marenzelleria viridis* in selected waters along the southern Baltic Sea. Dots indicate sampling sites. Note differences in density scaling between maps.

### *Distribution in the Darss-Zingst Bodden and the Oder Estuary*

Fig. 4 shows detailed distribution maps of *M. viridis* for the Darss-Zingst Bodden and the Oder Estuary in summer 1993. Maximum densities were revealed in the middle of the Darss-Zingst Bodden and in the south of the Oderhaff (10 000 and 28 000 ind. m$^{-2}$, respectively). High density values of inner coastal waters were restricted to sites near the coastline and less than 2 m depth. The species was often generally absent from the deeper central parts of the lagoons (3-5 m). Stations studied in the Pomeranian Bay ranged from 6-20 m depth. No relationship was observed between abundance and depth. High densities of about 3 500 ind. m$^{-2}$ were found only in the Southwest of the bay, close to river mouths. Numbers decreased rapidly with increasing distances from the shore. Only single specimens were recovered at the northern edge to the adjacent Arkona Basin.

Comparable weight measurements were available for a few stations only. Highest biomass values of 8-9 g AFDW m$^{-2}$ were found in the southwestern part of the Pomeranian Bay. Biomass values ranged from 0.2-1.3 g AFDW m$^{-2}$ offshore. Wet weight measurements from the Darss-Zingst

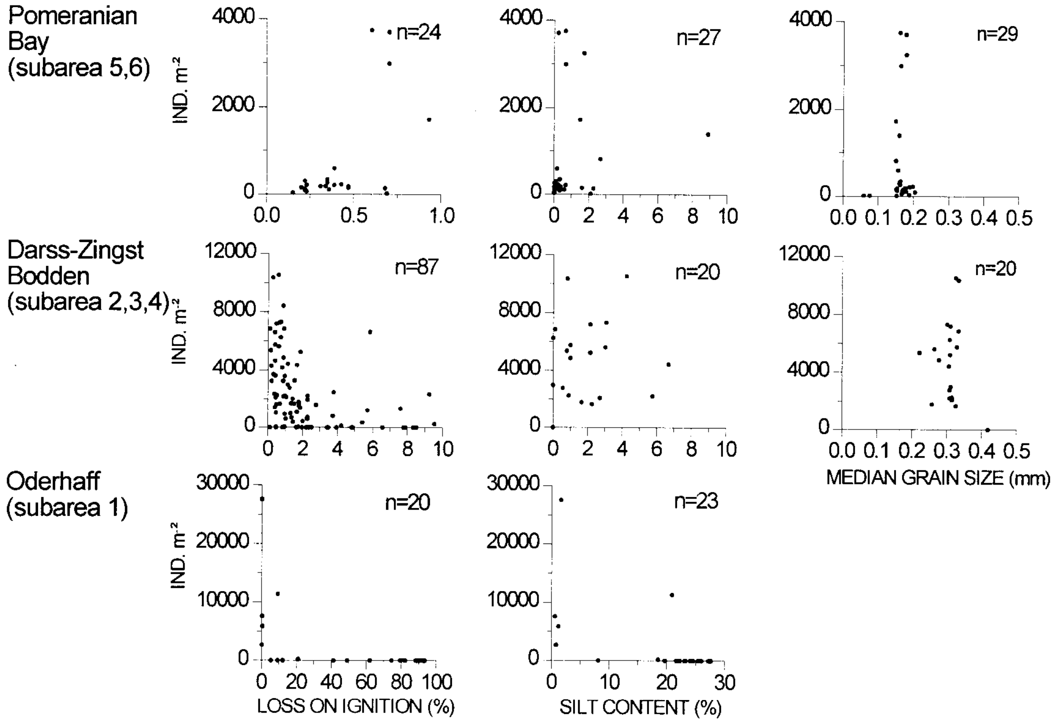

Fig. 5: Relationship between density of *Marenzelleria viridis* and sediment parameters in different subareas.

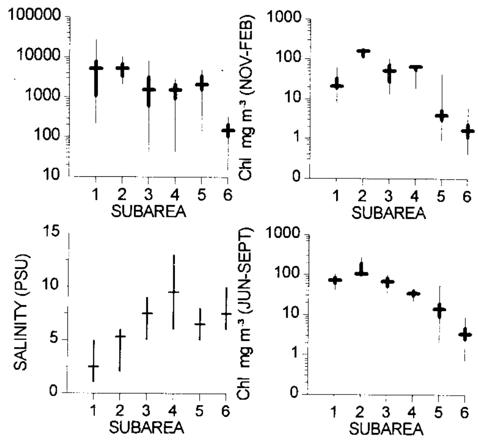

Fig. 6: Median densities of *Marenzelleria viridis* (zero values excluded), annual mean salinity, median summer concentration of chlorophyll *a* and median winter concentration of chlorophyll *a* in six subareas along the southern Baltic. Thick lines indicate quartiles, thin lines indicate minimum and maximum. Note logarithmic scaling of three Y-axes.

Bodden were transformed into AFDW by own conversion factors. Mean values ranged from 30-40 g AFDW m$^{-2}$ (maximum 70 g AFDW m$^{-2}$).

### *Environmental factors*

The relationship between abundance and sediment parameter is given for samples from the Pomeranian Bay, the Darss-Zingst Bodden and the Oderhaff collected during summer 1993 (Fig. 5). Adult *M. viridis* occurred in sediments with an organic content between 0.1 and 10 % and a silt content between 0 and 10 %. The median grain size of colonized sediments ranged from 0.05 to 0.35 mm. Large differences occurred between the subareas in the range of the sediment types investigated. Whereas sediments in the Pomeranian Bay were found to be almost sandy with an organic content below 1 % of sediment DW, a great variety of sandy and muddy sediments was encountered in inner coastal waters. Stations differed substantially in organic content and silt content of the substrate, but not in median grain size.

Salinities of the subareas ranged from 1.7 to 14 ‰ in 1993 and were lowest in the Oderhaff (subarea 1). Fig. 6 shows that highest values of more than 10 ‰ were measured in the eastern part of the Darss-Zingst Bodden (subarea 4) and in the Northwest of the Pomeranian Bay (subarea 6).

No intra-annual cyclic variation was found for the chlorophyll *a* content of the shallow lagoons in the Darss-Zingst Bodden. Median values ranged from 25 to 105 mg Chl *a* $m^{-3}$. The chlorophyll concentration decreased from the west (subarea 2) to the east (subarea 4) of the Bodden chain. Similar high values were found in the Oderhaff (subarea 1) during summer, but concentrations decreased in winter. The median winter concentration of chlorophyll *a* was only 13 mg $m^{-3}$. The lowest chlorophyll concentrations were found in the Pomeranian Bay (subareas 5, 6). Median summer values were 11 and 2.3 mg Chl *a* $m^{-3}$, respectively. Winter values appeared to be even lower (4.3 and 1.8 mg Chl *a* $m^{-3}$, respectively).

### *Population dynamics*

Fig. 7 presents the dynamics of the total population density of six sites from April 1993 to October 1994. Only subarea 2 showed a clear increase in total density within the time period under investigation. Salinity increased in subarea 2 from about 2 ‰ in 1992 to about 5 ‰ in 1993. A successful recruitment of larvae in autumn 1993 caused the exponential increase in densities (see also Fig. 8). Only slight temporal variation of abundances was observed at all other sites.

Fig. 8 shows the details of the population dynamics of selected single sites from the same subareas. We selected sites with the largest n-values for presentation, because there was no difference in the population dynamics between sites within a certain subarea. Subarea 4 was not investigated.

A clear annual life cycle was observed in the Darss-Zingst Bodden in subareas 2 and 3. Settlement of larvae took place in late autumn. Juveniles were growing fast. They grew to a width of about 1.2 mm by April 1993 and up to about 1 mm by April 1994. They reached a mean width of about 2.1 mm in September and could not be distinguished from adult cohorts by width measurements in winter (about 2.5 mm mean width of adults). Two different adult cohorts were distinguished by a difference in the number of segments with large gills between one and two year old specimens. Whereas the large gills of one year old worms appeared only within the first 40-50 segments, large gills of two year old worms reached up to the 60th segment (Zettler, own obs.). The maximum width of adults was 3.1 mm.

Only few first year worms were found in the Oderhaff in 1993/94 (subarea 1). Older cohorts occurred throughout the year and grew to a mean width of 2.5 mm (maximum 3.1 mm).

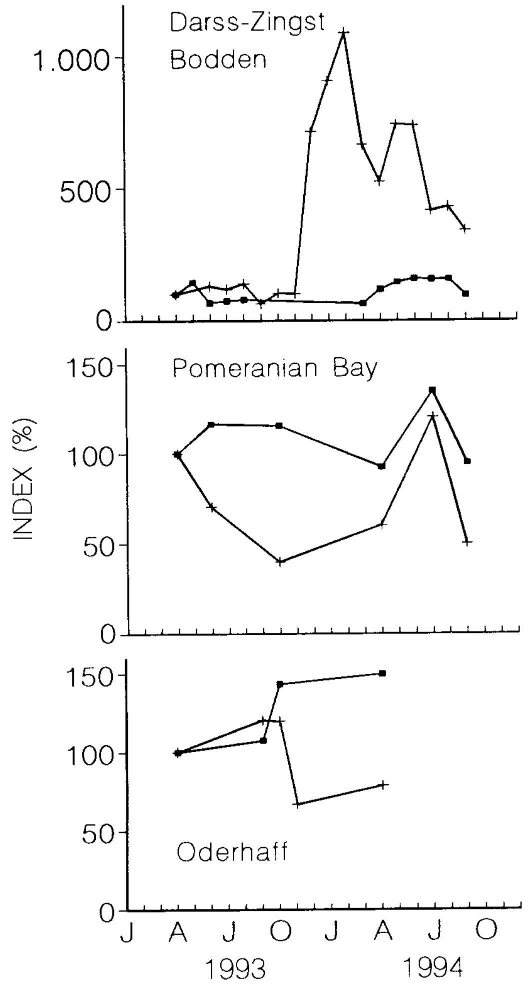

Fig. 7: Population trends of *Marenzelleria viridis* at two sampling sites from three different subareas along the southern Baltic. 100 % values of the population-index: Darss-Zingst Bodden: 5 223 ind. $m^{-2}$ - squares; 7 176 ind. $m^{-2}$ - crosses, Pomeranian Bay: 148 ind. $m^{-2}$ - squares, 3 244 ind. $m^{-2}$ - crosses; Oderhaff: 2 558 ind. $m^{-2}$ - squares, 4 226 ind. $m^{-2}$ - crosses.

First year specimens were found occasionally in the offshore part of the Pomeranian Bay (subarea 6). Two year old specimens seemed to be dominant. The largest worm ever found was 2.6 mm in width. The mean width of adults was about 2.2 mm.

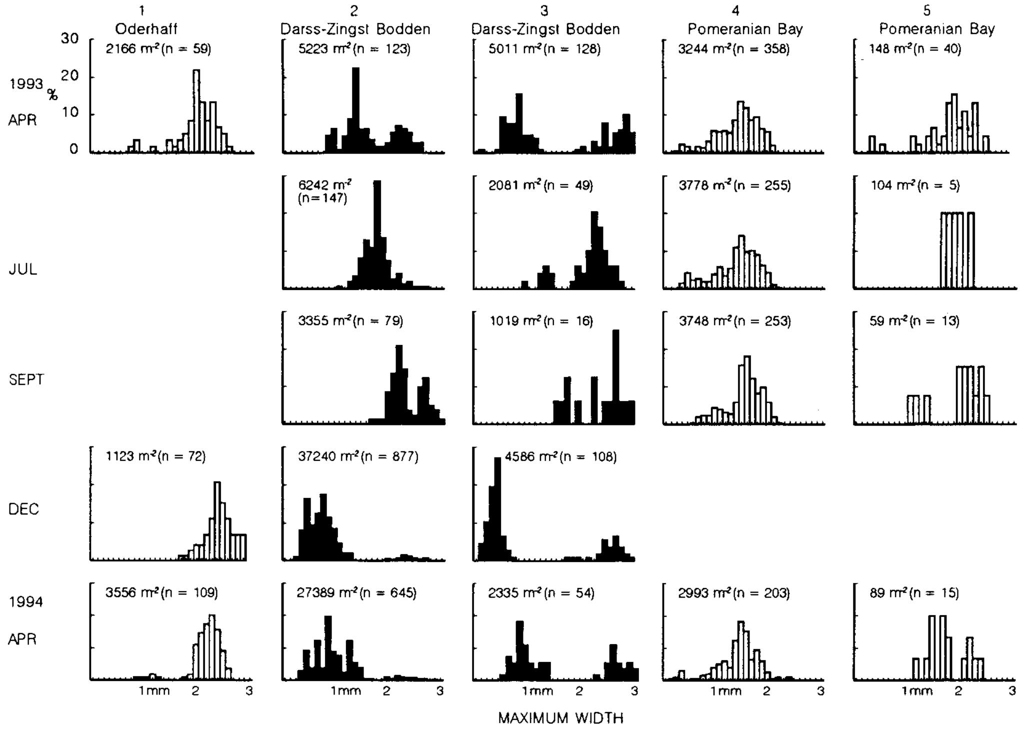

Fig. 8: Width-frequency histograms of five selected subareas along the southern Baltic from April 1993 to April 1994. Filled bars indicate sites with successful larval settlement in the Darss-Zingst Bodden, open bars indicate a site at the mouth of Oder River with weak recruitment and sites in the Oderhaff and the offshore part of the Pomeranian Bay where recruitment has failed. Note also differences in maximum width between inshore and offshore waters.

An inverse population structure with low numbers of first year worms and large numbers of adult worms was found at coastal sites in the Pomeranian Bay (subarea 5). Three cohorts could be distinguished for all seasons. No other variation than a slight increase of adult cohorts in late summer was observed throughout the year. Juveniles grew only to a mean width of 1.1 mm within the first year of life. Adult worms usually did not exceed a mean width of 1.8 mm. The maximum width of adults was once 2.2 mm and 2.4 mm, respectively. Separation of adult cohorts was not investigated.

## DISCUSSION

Species are known to be distributed along natural gradients of environmental factors. Gradients of several factors usually overlap each other. The importance of a single factor for the regulation of the density of a species follows an optimum curve or a saturation curve. The realized niche depends on the combination of all important factors. The character of the minimum factor changes spatially and temporally due to kind of overlap in many different environmental factors. Hence, the acceptable range of a single factor may change between areas and times in relation to the prevailing composition of other factors (Gray 1984).

During our investigation we discovered *M. viridis* in a wide range of brackish habitats. It propagated in semi-enclosed shallow lagoons as well as in coastal zones and offshore bays. Thus, the species occurred in areas exhibiting also a wide range of environmental conditions. The following account will describe the realized pattern of optimum or saturation curves of environmental factors in the southwestern Baltic Sea in relation to data available from experimental studies.

*Salinity*

*M. viridis* was found during this study at salinities of almost 1 ‰ and up to almost 15 ‰. Abundances were highest at salinities of around 5-8 ‰ and decreased rapidly above 10 ‰. A low salinity range from 2 to 8 ‰ was reported also for the eastern Baltic Sea by ZMUDZINSKI & al. (1993). Salinity of interstitial water at the Ems Estuary varied between 5 and 17 ‰ (ESSINK & KLEEF 1993). The species is most frequently found in areas of reduced salinities in North America. It is known to dominate the salinity range between 0.5 and 15 ‰ (BOESCH 1977; DOERJES & HOWARD 1975).

Early larval stages are unable to develop at salinities of less than 5 ‰. The growth of older larvae ceases, according to GEORGE (1966) and BOCHERT & BICK (1995). These experimental studies were confirmed by our population studies in the Oderhaff at salinities between 1 and 4 ‰. Although, high densities of planktonic larvae were reported for the Oderhaff by GRUSZKA (1991b), no successful settlement of juveniles was observed. Most likely, the larvae were drifted occasionally into the Oderhaff by strong water influxes from the Pomeranian Bay during storms (LAMPE 1993). The absence of juveniles in the offshore part of the Pomeranian Bay can not be explained by this factor, because no significant differences were found between the salinities of all other subareas.

We are unable to explain why adult stages did not occurred in the southwestern Baltic Sea at salinities above 15 ‰. There are some indications from recent experimental studies that adult worms, adapted to the horohalinicum, avoid salinities above 15 ‰. FRITZSCHE (1995) reported hyperosmoregulation by this polychaete for a salinity range between 0 and 30 ‰. He also recorded a 50 % mortality rate of adult stages, adapted to salinities of 5 ‰, at a salinity of almost 30 ‰. From this it can be concluded that *M. viridis* is a typical genuine brackish water species, well adapted to the horohalinicum (KINNE 1971; ARNDT 1989).

*Water depth*

At present, *M. viridis* inhabits depths between 0.2 and 30 m in the southwestern Baltic with a maximum nearshore at depths below 2 m. ZMUDZINSKI & al. (1993) recorded the polychaete down to 50 m with a maximum of 20-30 m in the eastern part of the Baltic Sea. The deepest observations of single adult specimens from the Baltic ranged down to 90 m in the Bornholm Basin (own obs. in 1993). The lower depth range of the species in the southwestern Baltic Sea was probably caused by high salinity values of the bottom water at 20-25 ‰ after a massive salt water influx from the North Sea in January 1993 (NEHRING & al. 1994).

*Sediment type*

Adult *M. viridis* inhabit vertical J-shaped, mucus-lined burrows with a mean diameter of about 2 mm. The depth of the burrow is governed mainly by sediment type: the more sandy or muddy the substrate, the smaller the depth (DAUER & al. 1981; ZETTLER & al. 1994). Tubes were generally deeper in sand than in mud (HINES & COMTOIS 1985).

Water content and grain size of the substrate are important factors for burrowing polychaetes (e.g. ESSELINK & ZWARTS 1989). A high water content is likely to be unfavourable for the stability of the unbranched burrows of *M. viridis*. An increase in water content of the substrate is usually correlated with an increase in organic- and silt content (SCHLUNGBAUM & al. 1994b). Adult worms from the southwestern Baltic Sea were restricted to sediments with an organic content below 5 %. They never occurred in sediments with an organic content above 10 %. Similar values were found for the silt content. No lower limit was observed. KINNER & al. (1974) reported major occurrences in sediments of 0-25 % silt content from a North American Estuary.

Silty sediments with high organic contents were restricted to the central parts of the semi-enclosed lagoons under investigation. Due to the effects of eutrophication large oxygen amplitudes occurred there during summer (LAMPE 1993, SCHLUNGBAUM & al. 1994b; own measurements). In contrast, nearshore areas of the lagoons were sandy and well oxygenated in most cases. As described above, *M. viridis* inhabited mainly shallow sandy nearshore parts of inner coastal waters and was often absent from the deeper central parts. The impact of temporal events of oxygen deficiency and formation of sulphide in the muddy central areas on densities of *M. viridis* is unclear. The spionide has remarkable adaptation strategies enabling it to live under such inhospitable conditions (FRITZSCHE & von OERTZEN 1995). Oxygen depletion of about 20 days were observed to reduce abundances in the Pomeranian Bay in summer 1994, especially of first year specimens.

Also, coarse gravel might cause negative effects on penetrability and stability of the substrate. The lower and upper value of the vulnerable grain size was not measured precisely during this study. No preferred grain size range was found between 0.15 and 0.35 mm median grain size. Only two sites with a median grain size below 0.1 and above 0.4 mm were studied. Single worms were found at these sites.

*Food supply*

Polychaetous annelids of the family *Spionidae* feed at the sediment-water interface with a single pair of tentaculate palps. They have been classified as selective surface deposit-feeders as well as suspension-feeders (Hempel 1957; Fauchald & Jumars 1979). Due to the available food supply, *M. viridis* can utilize particles both in suspension and from sediment surface (Dauer & al. 1981). If no suspended particles are available, both palps stay in contact with the sediment surface. Palps are lashing in the water column when suspended particles occur. Individuals from muddy sediments were observed to continue surface deposit-feeding even when suspended particles were available. The worms significantly increase the rate of defecation when suspended particles are present (Dauer & al. 1981, own laboratory observ.).

Qualitative and quantitative observations on the food composition of *M. viridis* from the southwestern Baltic Sea revealed mainly planktonic algae from all semi-enclosed lagoons. Fresh phytoplankton and resuspended organic material are the most important food sources. Sand gravel was a considerable part of the material found in intestines too. Specimens of the Pomeranian Bay mainly contained sand. A minor part of fresh phytoplankton was found only near river mouths (R. Burckhardt & B. Meyer-Harms, pers. commn; own observ.).

However, fresh phytoplankton is supposed to be the most important food source of *M. viridis*. Therefore, abundances of this spionid still can be related to the feeding biology. Water phytoplankton concentration can be used to describe the food supply, because the water column in shallow coastal waters is usually well mixed by wind forcing down to the bottom. Our observations indicate a clear positive relationship between distribution, abundances, population dynamics, and growth rate and the phytoplankton concentration of the water column. Abundances of adult stages were about ten times higher in inner coastal waters than in offshore parts of the Pomeranian Bay (10 000-20 000 ind. $m^{-2}$ and 100-200 ind. $m^{-2}$, respectively). The same difference was found for the chlorophyll concentration (50-100 mg Chl *a* $m^{-3}$ and 3-5 mg chl *a* $m^{-3}$, respectively). Maximum widths and growth rates were much greater in the semi-enclosed lagoons than in the Pomeranian Bay too. No successful settlement of juveniles was found in offshore parts of the Pomeranian Bay with winter chlorophyll *a* contents below 5 mg $m^{-3}$.

### *Outlook for future dispersal of M. viridis*

Since this North American polychaete was found in the Baltic Sea, it has proliferated very successfully. It has probably established itself permanently and has already become the dominating species in many horohaline coastal parts of the Baltic Proper. A similar process was observed in estuaries around the North Sea. The rapid dispersal can be explained by several causes. First of all, the species propagates in a wide range of horohaline to oligohaline extreme biotopes with periods of hypoxic and anoxic conditions. There are not many other large benthic invertebrates living in such environments within the Baltic Sea. *Nereis diversicolor* (O.F. Müller) is the only polychaete inhabiting the same areas. Within the horohalinicum until today no negative interspecific interactions were detected with other macrobenthic invertebrates (Zettler 1994; Zettler & Bick 1996).

Due to the effects of eutrophication, primary production is extraordinary high in Baltic estuaries (e.g. Wasmund & Schiewer 1994). No food shortage will limit the phytoplankton feeding spionide because of the absence of large filter-feeding bivalves in horohaline waters. Competition for food is likely to occur in oligohaline waters with mussel beds of *Dreissena polymorpha* and in coastal offshore parts with high densities of filter-feeding bivalves, *Mytilus edulis* (L.) and *Mya arenaria*. Bivalves are also known to reduce the recruitment rate of larvae (Hines & al. 1989).

The motility of older larval stages and benthic stages is important for the species success too. Adult stages were found in the southwestern Baltic up to 50 km away from successful recruitment areas. The phenology and causes of planktonic phases in the Baltic Sea have not been properly investigated yet. The life cycle of North American *M. viridis* involves three planktonic phases: a juvenile dispersal up the estuary, an adult dispersal down the estuary and a spawning phase (Dauer & al. 1982). Dauer & al. (1981) observed intensive movements of worms in relation to food supply.

The enormous production of larvae (Bochert & al. 1993) is probably the reason for the rapid speed of dispersal. The chance of the larvae to survive a ballast water ship transport to the receiving ecosystem is high. Transport distances are short within the Baltic. Most of the Baltics′ harbours are horohaline brackish and eutrophicated. It is precisely in such areas, that alien species are numerous (Leppäkoski 1984; Jansson 1994).

## ACKNOWLEDGEMENTS

This study was supported by the Federal Ministry of Research and Technology (BMBF) under grants number 03F0031A, 03F0105B and 03F0095C. H. Rumohr, V. Schrören and J. Warzocha kindly provided part of the data. We thank R. Bastrop and M. Röhner for information on the genetics of *M. viridis*. We would like to thank also A. Bick and B. Günther for their help during any stage of this study.

## REFERENCES

Arndt, E.A. 1989. Ecological, physiological and historical aspects of brackish water fauna distribution. – Pp. 327-337 in: Ryland, J.S. & P.A. Taylor (eds). *Reproduction, genetics and distribution of marine organisms.* 23rd European Marine Biology Symposium. Olsen &Olsen, Fredensborg.

— 1994. Struktur und Dynamik des Makrozoobenthos in der Darss-Zingster Boddenkette im Laufe der letzten 25 Jahre unter besonderer Berücksichtigung der Makrozoobenthos-Entwicklung im Saaler Bodden von 1986-1990. – *Rostocker Meeresbiologische Beiträge* 2:93-120.

Bastrop, R., M. Röhner & K. Jürss 1995. Are there two species of the polychaete genus *Marenzelleria* in Europe ? – *Marine Biology* 121:509-516.

Bick, A. & R. Burckardt 1989. Erstnachweis von *Marenzelleria viridis* (Polychaeta, Spionidae) für den Ostseeraum, mit einem Bestimmungsschlüssel der Spioniden der Ostsee. – *Mitteilungen aus dem Zoologischen Museum Berlin* 65:237-247.

Bochert, R. & A. Bick 1995. Der Einfluß von Salzgehalt und Temperatur auf die Larvalentwicklung von *Marenzelleria viridis* (Polychaeta: Spionidae). – *Verhandlungen der Deutschen Zoologischen Gesellschaft* 88:21.

Bochert; R., A. Bick, M.L. Zettler & E.A. Arndt 1993. *Marenzelleria viridis* (Verrill, 1873) (Polychaeta, Spionidae) an invader in the benthic community in Baltic coastal inlets – investigations of the reproduction. – *Proceedings of the 13. BMB-Symposium, Riga, Latvia*: in press.

Boesch, D.F. 1977. A new look at the zonation of benthos along the estuarine gradient. – Pp. 245-266 in: Coull, B.C. (ed.). *Ecology of marine benthos.* University of South Carolina Press, Columbia.

Carlton, J.T. 1985. Transoceanic and interoceanic dispersal of coastal marine organisms: the biology of ballast water. – *Oceanography and Marine Biology an Annual Revue* 23:313-371.

Dauer, D.M., R.M. Ewing, J.W. Sourbeer, W.T. Harlan & T.L. Stokes 1982. Nocturnal movements of the macrozoobenthos of the Lafayette River, Virginia. – *Internationale Revue der gesamten Hydrobiologie* 67:761-775.

Dauer, D.M., C.A. Maybury & R.M. Ewing 1981. Feeding behaviour and general ecology of several spionid polychaetes from the Chesapeake Bay. – *Journal of Experimental Marine Biology and Ecology* 54:21-38.

Dörjes, J. & J.D. Howard 1975. Estuaries of the Georgia coast, USA: Sedimentology and biology. IV. Fluvial-marine transition indicators in an estuarine environment, Ogeechee River-Ossabaw Sound. – *Senkenbergiana maritima* 7:137-179.

Esselink, P. & L. Zwarts 1989. Seasonal trend in burrow depth and tidal variation in feeding activity of *Nereis diversicolor*. – *Marine Ecology Progress Series* 56:243-254.

Essink, K. & H.L. Kleef 1988. *Marenzelleria viridis* (Verrill, 1873) (Polychaeta: Spionidae): a new record from the Ems Estuary (The Netherlands/Federal Republic of Germany). – *Zoologische Bijdragen (Leiden)* 38:31-43.

— 1993. Distribution and life cycle of the north American spionid polychaete *Marenzelleria viridis* (Verrill, 1873) in the Ems estuary. – *Netherlands Journal of Aquatic Ecology* 27:237-246.

Fauchald, K. & P.A. Jumars 1979. The diet of worms: a study of polychaete feeding guilds. – *Oceanography and Marine Biology an Annual Revue* 17:193-284.

Fritzsche, D. 1995. Leistungsanalytische und resistenzökologische Untersuchungen zur Emanzipation des Polychaeten *Marenzelleria viridis* (Verrill 1873) gegenüber den Faktoren Salinität und Sauerstoffpartialdruck. PhD-thesis, University of Rostock, Rostock.

Fritzsche, D. & J.A. von Oertzen 1995. Metabolic response to changing environmental conditions in the brackish water polychaetes *Marenzelleria viridis* and *Hediste diversicolor*. – *Marine Biology* 121:693-699.

George, J.D. 1966. Reproduction and early development of the spionid polychaete, Scolelepis viridis (Verrill). – *The Biological Bulletin* 139:76-93.

Gray, J.S. 1984. *Ökologie mariner Sedimente.* – Springer-Verlag, Berlin. 193 pp.

Gruszka, P. 1991a. *Marenzelleria viridis* (Verrill, 1873) (Polychaeta: Spionidae) – a new component of shallow water benthic community in the southern Baltic. – *Acta Ichthyologica et Piscatoria* 21 Suppl.:57-65.

– 1991b. *Marenzelleria viridis* keeps conquering the Baltic Sea. – *12th Baltic Marine Biologists Symposium. August 23-30, 1991, Helsingør, Denmark.* Abstracts of poster:14.

HELCOM 1988. Guidelines for the Baltic Monitoring Programme for the third stage. Part D. Biological Determinants. – *Baltic Sea Environmental Proceedings* , 27 D. 161 pp.

Hempel, C. 1957. Über den Röhrenbau und die Nahrungsaufnahme einiger Spioniden (Polychaeta, Sedentaria) der deutschen Küsten. – *Helgoländer wissenschaftliche Meeresuntersuchungen* 6:100-135.

Hines, A.H. & K.L. Comtois 1985. Vertical distribution of infauna in sediments of a subestuary of central Chesapeake Bay. – *Estuaries* 8:296-304.

Hines, A.H., M.H. Posey & P.J. Haddon 1989. Effects of adult suspension-feeding bivalves on recruitment of estuarine infauna. – *The Veliger* 32:109-119.

Jansson, K. 1994. *Alien Species in the marine environment – introductions to the Baltic Sea and the Swedish west coast.* – Swedish Environmental Protection Agency, Report 4357, Solna. 68 pp.

Jeffrey, S.W. & G.F. Humphrey 1975. New spectrophotometric equations for determining chlorophylls a, b, $c_1$ and $c_2$, in higher plants, algae and natural phytoplankton. *Biochemie und Physiologie der Pflanzen* 167:191-194.

Kinne, O. (ed.) 1971. *Marine ecology* 1, Part 2. – Hamburg, Biologische Anstalt Helgoland. Pp. 683-1244.

Kinner, P., D. Mauer & W. Leathem 1974. Benthic invertebrates in Delaware Bay: animal sediment associations of the dominant species. – *Internationale Revue der gesamten Hydrobiologie* 59:685-701.

Lampe, R. 1993. Environmental state and material flux in the western part of the Oder river estuary – results and consequences. – *Petermanns Geographische Mitteilungen* 137:275-282.

Leppäkoski, E. 1984. Introduced species in the Baltic Sea and its coastal ecosystems. – *Ophelia* Suppl. 3:123-135.

– 1991. Introduced species – recource or threat in brackish-water areas? Examples from the Baltic and the Black Sea. – *Marine Pollution Bulletin* 23:219-223.

McLusky, D.S., S.C. Hull & M. Elliott 1993. Variations in the intertidal and subtidal macrofauna and sediments along a salinity gradient in the upper Forth Estuary. – *Netherlands Journal of Aquatic Ecology* 27:101-109.

Nehring, D., W. Matthäus, H.-U. Lass, G. Nausch 1994. Hydrographisch-chemische Zustandseinschätzung der Ostsee 1993. – *Meereswissenschaftliche Berichte* 7:1-68.

Norkko, A., E. Bonsdorff & C. Boström 1993. Observations of the polychaete *Marenzelleria viridis* (Verrill) on a shallow sandy bottom on the south coast of Finland. – *Memoranda Societa Fauna Flora Fennica* 69:112-113.

Persson, L.-E. 1990. The national Swedish environmental monitoring programme (PMK): soft macrofauna monitoring off the south coast of Sweden-Annual Report 1990. – *Naturvardsverket, Rapport* 3937:5-12.

Powilleit, M. J. Kube, J. Maslowski & J. Warzocha 1996. Distribution of macrobenthic invertebrates in the Pomeranian Bay (Southern Baltic Sea) in 1993/94. *Bulletin of the Sea Fisheries Institute, Gdynia-Poland* 3:75-87.

Prena, J.& F. Gosselck 1989. Das Makrozoobenthos eines hocheutrophierten Küstengewässers – Eine Bonitierung der Wismarer Bucht (westliche Ostsee). – *Fischerei-Forschung* 27:51-56.

Schlungbaum, G., H. Baudler & G. Nausch 1994a. Die Darss-Zingster Boddenkette – ein typisches Flachwasserästuar an der südlichen Ostseeküste. – *Rostocker Meeresbiologische Beiträge* 2:5-26.

– 1994b. Sedimentstruktur und Sedimentdynamik in den Darss-Zingster Boddengewässern. – *Rostocker Meeresbiologische Beiträge* 2:27-40.

Wasmund, N. & U. Schiewer 1994. Überblick zur Ökologie und Produktionsbiologie des Phytoplanktons der Darss-Zingster Boddenkette (südliche Ostsee). – *Rostocker Meeresbiologische Beiträge* 2:41-60.

Zettler, M.L. 1994. Immigration und Ausbreitung eines nordamerikanischen Polychaeten in ein inneres Küstengewässer der südlichen Ostsee und Auswirkungen auf das autochtone Makrozoobenthos. – *Erweiterte Zusammenfassung der Jahrestagung der Deutschen Gesellschaft für Limnologie e.V., Hamburg*, Bd. 2:659-699.

Zettler, M.L. & A. Bick 1996. The analysis of small- and mesoscale dispersion patterns of *Marenzelleria viridis* (Polychaeta: Spionidae) in a coastal water area of the southern Baltic. – *Helgoländer wissenschaftliche Meeresuntersuchungen* 50:265-286.

Zettler, M.L., A. Bick & R. Bochert 1995. Distribution and population dynamics of *Marenzelleria viridis* (Polychaeta: Spionidae) in a coastal water of the southern Baltic. – *Archive of fishery and marine research* 42:209-224.

Zettler, M.L., R. Bochert & A. Bick 1994. Röhrenbau und Vertikalverteilung von *Marenzelleria viridis* (Polychaeta: Spionidae) in einem inneren Küstengewässer der südlichen Ostsee. – *Rostocker Meeresbiologische Beiträge* 2:215-225.

Zmudzinski, L. 1993. Long-term changes in macrozoobenthos of the Vistula lagoon. – *2. Estuary Symposium; Estuarine environments and biology of estuarine species, Gdansk, Poland, October 18-22, 1993*, Abstract of poster.

Zmudzinski, L., S. Chubarova, Z. Dobrowolski, P. Gruszka, I. Fall, S. Olenin & N. Wolnomiejski 1993. Expansion of the spionid polychaete Marenzelleria viridis in the southern part of the Baltic Sea. – *Proceedings of the 13. BMB-Symposium, Riga, Latvia*: in press.

*Accepted 24 April 1996.*