

Distribution and population dynamics of *Marenzelleria viridis* (Polychaeta, Spionidae) in a costal water of the southern Baltic

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Abstract

The distribution of *Marenzelleria viridis* (Verrill 1873), a spionid polychaete imported from America during the 1980's, was studied in the chain of boddens south of the Darss-Zingst Peninsula between March 1992 and March 1993. Abundances were highest ($5\,000\text{ ind} \cdot \text{m}^{-2}$, wet wt = $400\text{ g} \cdot \text{m}^{-2}$) in the central part of the chain, where salinity was 5 to 7 PSU. Polychaete burrows were deepest (35 cm) in sandy substrates and decreased as the sediment became muddier or more densely packed. *M. viridis* built unbranched L- to J-shaped burrows with a single opening. Unlike the North Sea and North American populations, which do not reproduce until February/March, the population in the bodden chain started to reproduce in the autumn (September/October). The settlement of juvenile *M. viridis* with 17 to 19 setigers was observed throughout the bodden chain from mid-October onwards. Abundances were highest (mean: $150\,000\text{ ind} \cdot \text{m}^{-2}$ maximum: $270\,000\text{ ind} \cdot \text{m}^{-2}$) in the central part. Juveniles continued to colonize the sediment until January/February. Mortality exceeded the rate of settlement in early November, and the juvenile worm density decreased to between $3\,000$ and $6\,000\text{ ind} \cdot \text{m}^{-2}$ by March 1993. Larvae grew during the winter at all stations. Conditions appeared to be near optimal ($S = 5\text{ PSU}$) in the western part of the bodden chain, resulting in a three-fold increase in setiger number from about 20 to about 70 within five months. *M. viridis* has a life expectancy of at least two years, based on the two or three coexisting generations that could be distinguished from size distribution data.

Kurzfassung

Verteilung und Populationsdynamik von *Marenzelleria viridis* (Polychaeta, Spionidae) in Bodden der südlichen Ostsee

Die Verteilung von *Marenzelleria viridis* (Verrill 1873), eine in den 80er Jahren aus Nordamerika eingewanderten Spionide, wurde in der Boddenkette südlich der Halbinsel Darß-Zingst von März 1992 bis März 1993 untersucht. Die Spionide ist im gesamten Untersuchungsgebiet anzutreffen. Im

mittleren Bereich der Boddenkette, mit Salinitäten von 5-7 PSU, waren die Abundanzen am größten (6 000 - 8 500 Ind · m⁻², Feuchtmasse = 500 - 700 g · m⁻²). Es wurde der Einfluß des Sedimentes auf die Vertikalverteilung untersucht. Die maximale Eindringtiefe lag an sandigen Standorten bei 35 cm. Je schlückiger oder dichter gepackt das Substrat wurde, desto mehr nahm sie ab. *M. viridis* baut unverzweigte L- bis J-förmige Röhren mit einer Öffnung. Im Gegensatz zu den Populationen aus der Nordsee und von Nordamerika, die sich nicht vor Februar/März reproduzieren, beginnt die Population in der Boddenkette mit der Reproduktion im Herbst (September/Oktober). Das Festsetzen der juvenilen *M. viridis* mit 17 bis 19 Segmenten konnte ab Mitte Oktober beobachtet werden. Die Abundanzen waren im zentralen Bereich mit 150 000 Ind · m⁻² (max. 270 000 Ind · m⁻²) am größten. Die Neubesiedlung des Sedimentes dauerte bis zum Januar/Februar. Anfang November überstieg die Mortalität die Festsetzungsrate und die Dichten sanken auf 3 000 bis 6 000 Ind · m⁻² ab. An allen Stationen wurde während des Winters Wachstum beobachtet, jedoch konnten wir im westlichen Teil der Boddenkette mit einer Verdreifachung der Segmentzahl von 20 auf über 70 die höchste Wachstumsrate feststellen. *M. viridis* hat eine Lebenserwartung von über 2 Jahren. Mit Hilfe der Breitenmessung konnten 2 bzw. 3 koexistierende Generationen unterschieden werden.

Résumé

La distribution et la dynamique de populations de *Marenzelleria viridis* (Polychaeta, Spionidae) dans des étangs de la Mer Baltique du Sud

La distribution des *Marenzelleria viridis* (Verrill 1873) une spionide (Polychaeta, Spionidae) importée de l'Amérique du Nord pendant les années 80 a été étudiée dans la chaîne d'étangs au sud de la péninsule Darss-Zingst de mars 1992 à mars 1993. Les abondances étaient plus fortes dans la partie centrale de la chaîne (6 000 - 8 500 ind./m², Masse Mouillée = 500 - 700 g · m⁻²) où la salinité était de 5 à 7 PSU. Les percées étaient plus profondes (35 cm) dans les substrats sablonneux et diminuaient quand le sédiment devenait plus vaseux ou plus dense. *M. viridis* construit des tuyaux sans branches en forme de L ou de J avec une seule ouverture. Contrairement aux populations de la Mer du Nord ou de l'Amérique du Nord qui ne se reproduisent pas en février - mars, la population dans la chaîne d'étangs commence à se reproduire en automne (septembre - octobre). L'installation du *M. viridis* juvénile long de 17 à 19 anneaux a été observée dans la chaîne d'étangs à partir de la mi-octobre. Les abondances étaient plus fortes (min. 150 000 indiv./m², 270 000 indiv./m²) dans le centre. Les jeunes ont continué à coloniser le sédiment jusqu'à janvier-février. La mortalité excéda le taux d'installation au début de novembre et la densité des vers juvéniles diminua jusqu'à 3 000 et 6 000 indiv./m² au mois de mars 1993. Les larves ont crû pendant l'hiver dans toutes les stations. Les conditions furent presque optimales (S = 5 PSU) à l'ouest de la chaîne où le nombre d'anneaux tripla, passant de 20 à plus de 70 en 5 mois. *M. viridis* a une espérance de vie d'au moins 2 ans, résultat basé sur 2 ou 3 générations coexistantes qui ont pu être différenciées à partir de la taille des données de distribution.

Introduction

The spionid *Marenzelleria viridis* (Verrill 1873) (syn. *Scolecoplepides viridis*) originates from estuaries along the North American east coast. Its range extends from Newfoundland (Canada) to Georgia (USA) (32° to 60°N) (e.g. Foster 1971, George 1966, Maciolek 1984, Whitlatch 1981).

The first specimens reported in a European brackish water (the Forth estuary in Scotland) were found by McLusky et al. (1993) in 1982. The spionid spread rapidly in the North Sea. Essink and Kleef (1988) found it in the Ems estuary (Holland) in 1983, for instance, and Kirkegaard

(1990) in Ringkøbing Fjord (Denmark) in 1990. The first specimens in the Baltic Sea were discovered in the boddens south of the Darss-Zingst Peninsula by Bick and Burckhardt (1989) in 1985. In the Baltic Sea, too, the worm spread relatively rapidly, and was collected in Poland (Gruszka 1989) in 1988, Sweden (Persson 1991) in 1990 and Finland (Andersin pers. comm.) in 1990.

The present study describes the distribution of *M. viridis* in the bodden chain south of the Darss-Zingst Peninsula and compares the biotic and abiotic conditions found at the various stations in the boddens with those found in The North Sea and North American estuaries.

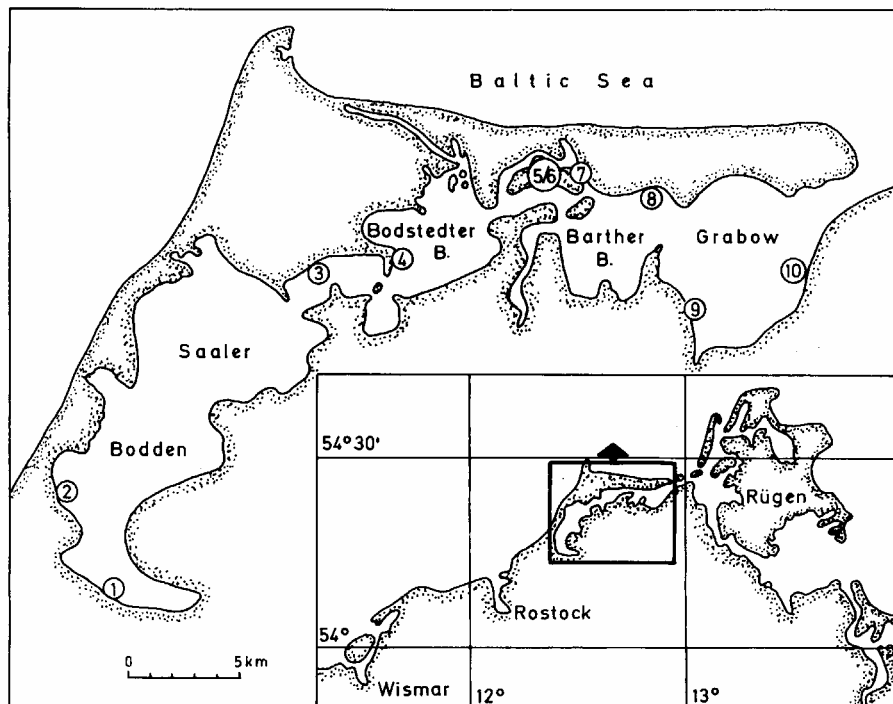


Figure 1: Area of investigation

Area of investigation

The investigation area (Fig. 1), the bodden chain south of the Darss-Zingst Peninsula, is situated north east of Rostock, has a length of about 40 km from west to east and occupies an area of 196.7 km² (Correns 1976). The salinity is subject to seasonal and interannual fluctuations owing to freshwater inflows and the open connection to the Baltic Sea (Arndt 1988). Mean annual salinities vary between 4 PSU in the west to 10 PSU in the east (Table 1). The mean depth is 2 m.

Table 1: Survey of the abiotic parameters at the stations during the investigation time

	stn. 1	stn. 2	stn. 3	stn. 4	stn. 5	stn. 6	stn. 7	stn. 8	stn. 9	stn. 10
salinity (PSU)	4.39	5.0	5.07	6.77	7.56	7.56	7.84	8.75	9.26	9.28
±	±	±	±	±	±	±	±	±	±	±
SD	0.87	0.45	1.01	1.09	1.02	1.02	2.15	1.59	0.71	0.58
organic content (%)	0.86	1.23	0.6	0.95	1.83	0.96	1.56	0.67	2.37	0.79
±	±	±	±	±	±	±	±	±	±	±
SD	0.53	0.69	0.52	0.53	0.65	0.26	0.36	0.55	1.22	0.33
mean grain size (mm)	0.27	0.28	0.23	0.27	0.23	0.29	0.25	0.27	0.17	0.36
±	±	±	±	±	±	±	±	±	±	±
SD	0.02	0.05	0.06	0.05	0.04	0.01	0.06	0.06	0.05	0.05
fraction < 0.063 mm (%)	1.75	3.99	2.06	2.58	5.2	0.86	2.81	1.47	13.1	2.48
±	±	±	±	±	±	±	±	±	±	±
SD	0.74	2.75	1.01	1.85	1.59	0.82	1.89	0.86	5.06	1.86

Methods

Stations 1 to 10 were selected so as to cover the whole salinity gradient and to take various sediment types into account. All stations were situated in shallow waters (0.5 to 1.2 m deep).

Core samples (3 per station) with a cross section of 78.5 cm² and penetration depth of 40 cm were collected at monthly intervals from March 1992 until March 1993 except at stations 1, 3 and 10, which were sampled every three months. The construction of the corer is described by Zettler (1993). The samples were passed through a 0.5 mm mesh sieve before being preserved in 4 % borax-buffered formalin. The samples were analyzed in the laboratory using a dissection microscope with a magnification of x10.

The organic content of the sediment was determined following combustion at 550 °C for 4 h. The mean grain size was ascertained by wet sieving using a set of sieves with the mesh sizes 1.0, 0.5, 0.2, 0.1 and 0.063 mm. The total biomass of the animals in each sample was weighed to the nearest 0.1 g wet weight and calculated for an area of 1 m².

During the reproductive period (from October 1992 onwards) owing to the smallness and high abundances of the juveniles we collected additional samples using a corer with a cross section of 11.95 cm² and a penetration depth of 5 cm. These samples were preserved before sieving (0.315 mm mesh).

The width measurements needed for the population dynamic studies of *M. viridis* were made at the widest point between 5th and 10th setiger.

Burrow shape was analyzed by means of various staining techniques (Löffler methylene blue, titanium yellow and neutral red). The cores (78.5 cm²) for studying the vertical distribution were divided into 5 cm slices, each slice being placed in a separate bucket. The slices were then sieved through sieves with a mesh size of 0.5 mm except when studying colonization by juveniles, in which case the top 10 cm were sieved through a mesh size of 0.315 mm.

Emergence traps were also employed for three months to study the swarming behaviour and migration of *M. viridis*. The construction of the emergence traps is described by Zettler (1993).

Results

Distribution of M. viridis

The stations differed substantially in salinity and organic content of the substrate, but not in mean grain size (Table 1). *M. viridis* was found everywhere in the bodden chain and was always present at all stations except the most easterly (about 9 PSU). Abundances were greatest at salinities of around 5 to 7 PSU in the central part of the bodden chain (Fig. 2).

M. viridis achieved mean abundances of 5 000 ind · m⁻² at stns. 3, 4 and 8 and of 2000 ind · m⁻² at stns. 6 and 7. In the oligohaline (S = 4 - 5 PSU) western part of the bodden chain (stns. 1 and 2), abundances varied between 1 000 and 2 000 ind · m⁻² during the course of the year. At the outlet from the bodden chain to the Baltic Sea, however, *M. viridis* was observed only sporadically, with mean abundances of 200 ind · m⁻².

Biomass increased continuously during the study at stn. 1 (Saaler Bodden), rising from 80g · m⁻² in March 1992 to 300 g · m⁻² in March 1993 (Fig. 3). The highest biomasses were found at stns. 3, 4 and 8 (up to 400 g · m⁻²). The wet weights at the stn. 3 and 4 increased during the study period, rising from 180 to 400 and 800 g · m⁻². A biomass peak was observed during the reproduction period (September to November) at stn. 4. The increase of 400 - 600 g · m⁻² is not accounted for by the appearance of juveniles.

M. viridis has become the dominant macrozoobenthos species within the bodden chain only a few years after its first appearance (Fig. 4). The spionid achieved its greatest density at stns. 3 and 4, where it composed over 80 % of the macrobenthic assemblage. Macrozoobenthos diversity in the investigation area increases as salinity increases towards the outlet to the Baltic Sea. *M. viridis* accounted for 40 % and 3 % of all macrobenthic individuals at stns 8 and 10 respectively. The subdominants at these stations were *Hediste diversicolor*, *Corophium volutator*, *Hydrobia* spp., *Cerastoderma lamarcki* and oligochaetes.

The burrows of *M. viridis* were L or J-shaped, unbranched and had a single opening (Zettler *et al.* 1994). Lined with a mucous layer and having a diameter of about 2 mm, they penetrated into the sediment to a depth of about 25 cm (maximum: 35 cm) (Fig. 5). Their depth was governed mainly by sediment quality: the more sandy or muddy the substrate, the shallower the depth.

The vertical distribution of *M. viridis* differed from that of *H. diversicolor* in that 90 % of the latter penetrated to a sediment depth of only 10 cm (maximum depth: 30 cm). No relationship was found between the burrow depth of *M. viridis* and the abundance of *H. diversicolor* (Zettler

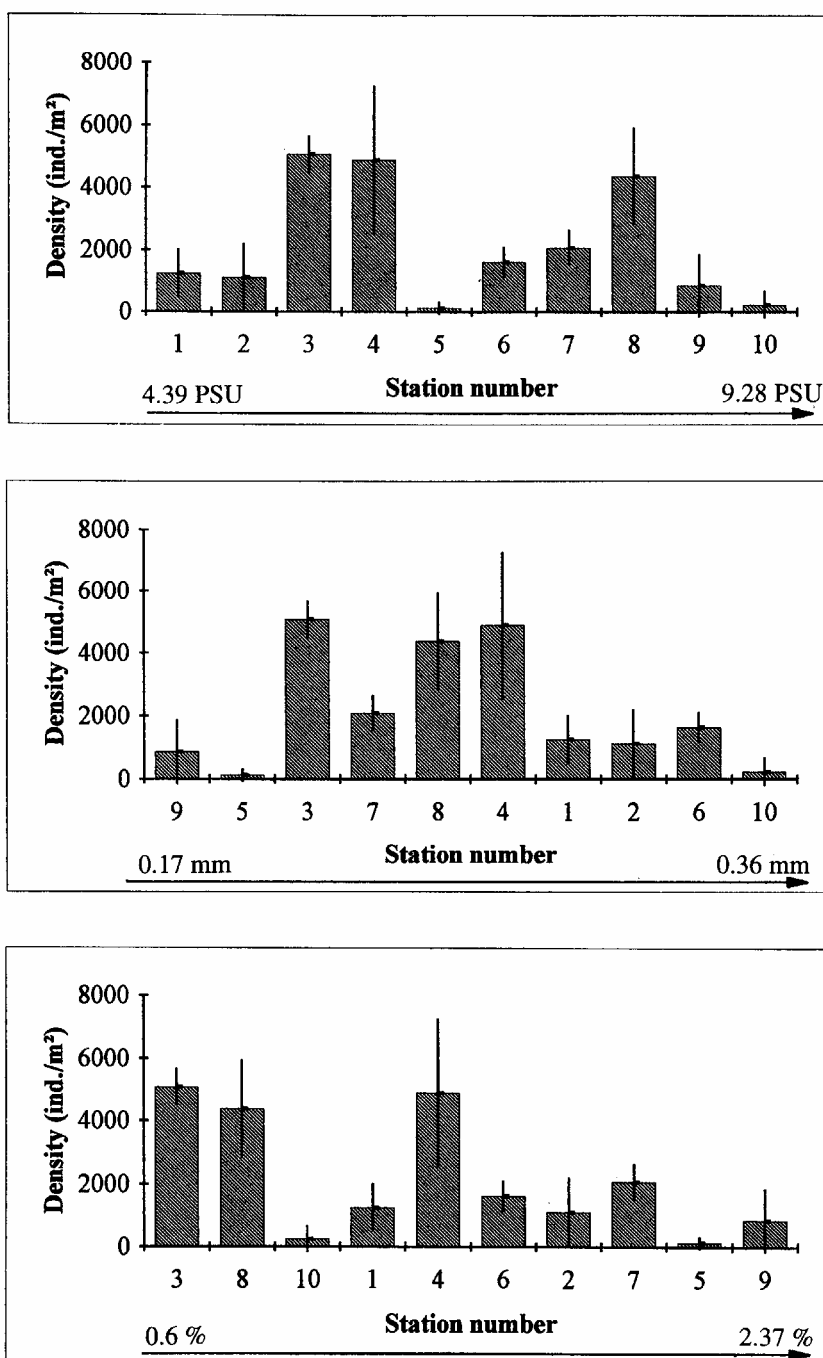


Figure 2: Densities of *M. viridis* at stns. 1-10 (ind · m⁻² means ± SD), a = at increasing salinities, b = in sediments with increasing mean grain sizes, c = in sediments with increasing organic contents

Marenzelleria viridis in southern Baltic

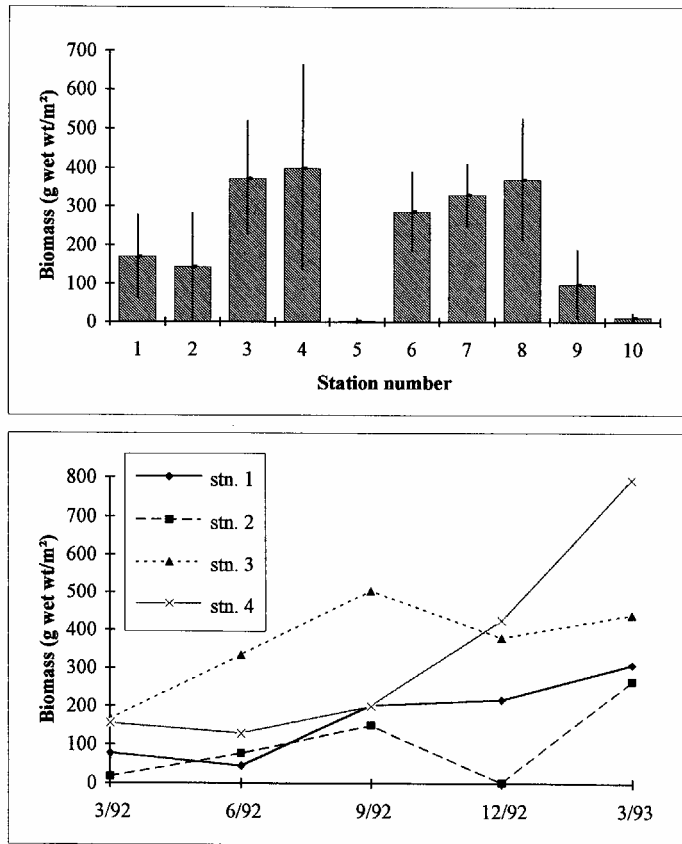


Figure 3: a = wet weights of *M. viridis* at stns 1-10 ($\text{g} \cdot \text{m}^{-2}$ means \pm SD), b = mean wet weights of *M. viridis* at stns. 1-4 from March 1992 to March 1993

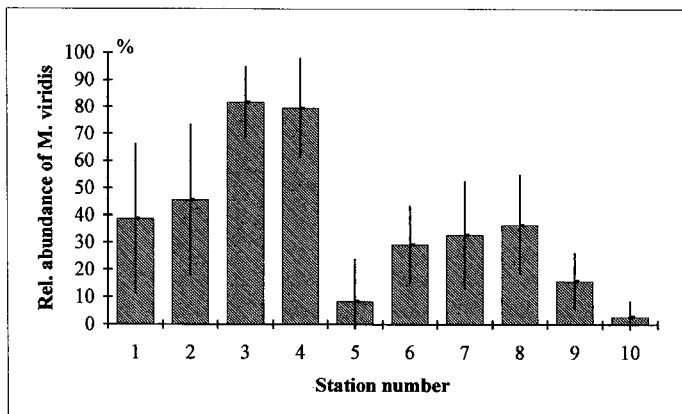


Figure 4: Relative abundances of *M. viridis* at stns. 1-10 (means \pm SD)

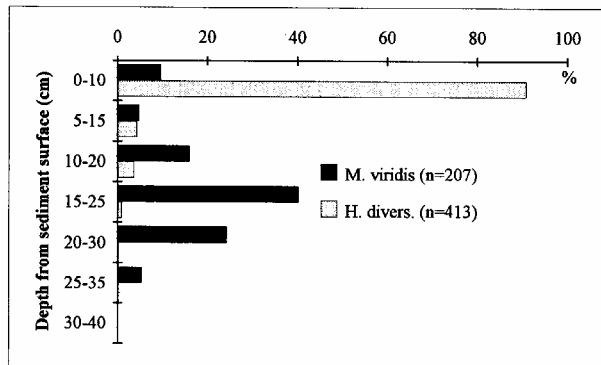


Figure 5: Vertical distribution of *M. viridis* and *H. diversicolor* at stn. 6

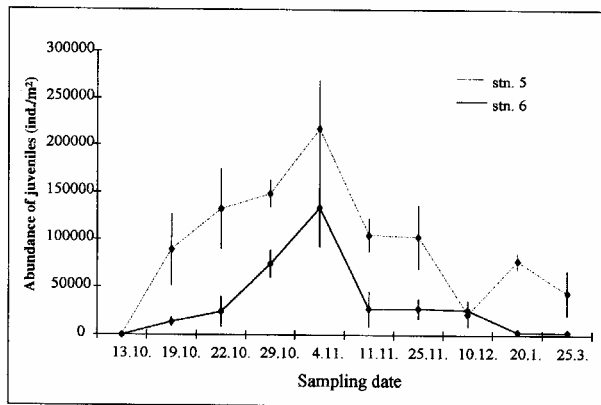


Figure 6: Abundances of juvenile *M. viridis* after settlement at stns. 5 and 6 (ind · m⁻² means ± SD) from October 1992 to March 1993

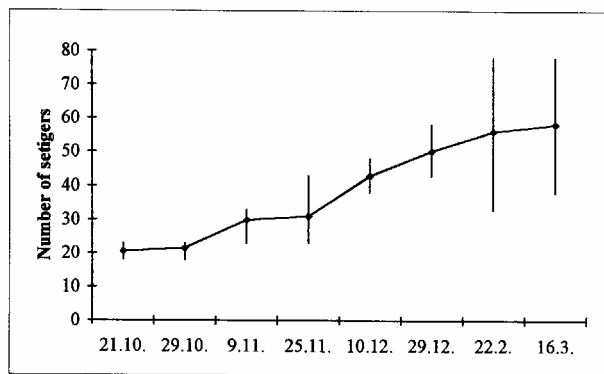


Figure 7: Growth of juvenile *M. viridis* at stn. 2 represented by average numbers of setigers, maximum and minimum

et al. 1994). Where burrows of *H. diversicolor* were present, the upper 4 to 5 cm of their ramified systems were also used by *M. viridis*. The spionids were oriented with their front ends pointing either upwards or downwards and were also able to turn round without leaving the burrow.

Emergence traps caught both adult (15 animals in three months) and juvenile (hundreds) *M. viridis* during our studies, thus proving that benthic stages were motile at least to some extent. We investigated the vertical distribution of the spionids five months after settlement, when the *M. viridis* juveniles had reached the 50 setiger stage. There was a distinct percentage increase of *M. viridis* in the top 10 centimetres, and this was accounted for almost exclusively by juveniles. Over 50 % of the worms were found in the top layer (0 - 10 cm).

Population dynamic of *M. viridis*

Juvenile *M. viridis* with between 15 and 19 setigers were observed to settle everywhere in the bodden chain from mid-October onwards. The lowest mean abundance of 6 000 ind/m² (max: 8 000 ind · m⁻²) was found in the western part (S ≈ 5 PSU), and abundances were also relatively low in the eastern part (50 000 ind · m⁻²). They were highest (mean: 150 000 ind · m⁻² max: 270 000 ind · m⁻²) in the central part of the bodden chain. The sediment appeared to be the decisive factor because, although stns. 5 and 6 were scarcely 10 m apart, they differed in organic content of sediment (Table 1) and also exhibited marked differences in colonization by juvenile *M. viridis* (Fig. 6). Settlement continued until January/February. However, mortality obviously exceeded the settlement rate in early November, and juvenile abundance decreased to 3 000 - 6 000 ind · m⁻² by March.

We analysed juvenile growth in terms of the mean numbers of setigers of animals at stn. 2, which is used here as example (Fig. 7). A larval settlement wave was observed throughout the investigation area in mid-October. Growth rates were highest at stn. 2 from mid-October to mid-March, the mean increase being 40 setigers (from 20 to 60, max: 78). Growth rates were lower (from 20 to 40) in the central part. About 90 % of the juveniles at stn. 2 had more than 50 setigers by March, 1993, whereas between 70 and 90 % were smaller than 50 setigers at the other stations.

Population dynamics were analysed at stn. 2 and 4, which had different salinities. Two generations were present at stn. 4 in the spring of 1992: adults from the 1990 reproduction phase and the growing juveniles from the previous year (Fig. 8). There were very few juveniles, however, and they were easily distinguishable from the adults, which had achieved their maximum width in September. Owing to the relatively fast growth of juvenile spionids in summer it was no longer possible to distinguish the two generations by means of their width in autumn. However, the low level of reproduction in 1991 can be deduced by comparing the proportion of juveniles found in the spring of 1992 and 1993. Only 4 % of the spionids found in March 1992 were juveniles, compared with 25 % in the following March. In 1992, reproduction at stn. 2 was so low that it could not be expressed quantitatively (Fig. 9). The number of juvenile *M. viridis* after the reproductive period was estimated in October 1992, and juveniles were found to be much more abundant than in the previous year. They grew to a width of over 1.2 mm by March 1993. No decline in the adult generation was observed. The changes in width

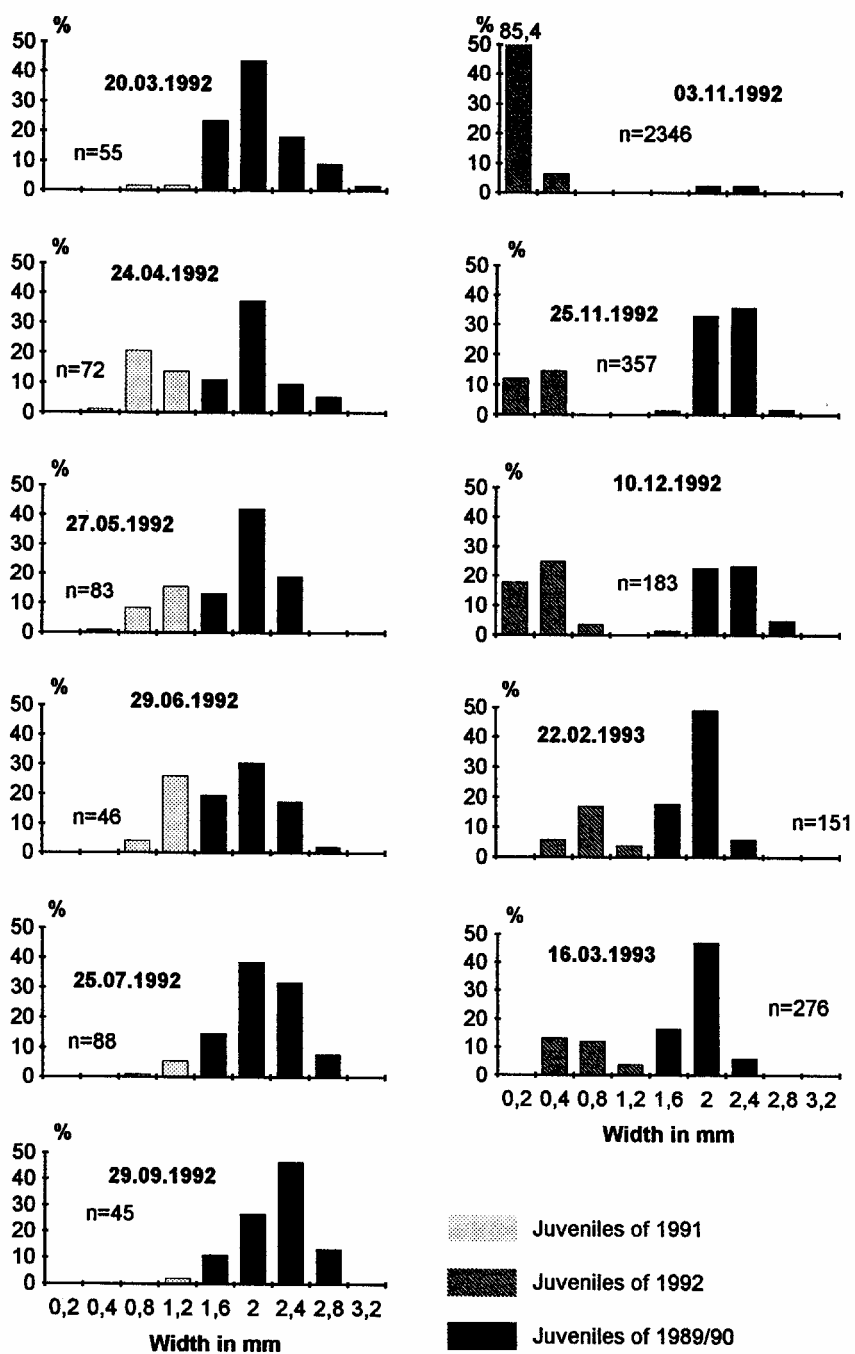


Figure 8: Size-frequency distribution of *M. viridis* at stn. 4 based on the greatest width (mm) between the 5th and 10th setiger

Marenzelleria viridis in southern Baltic

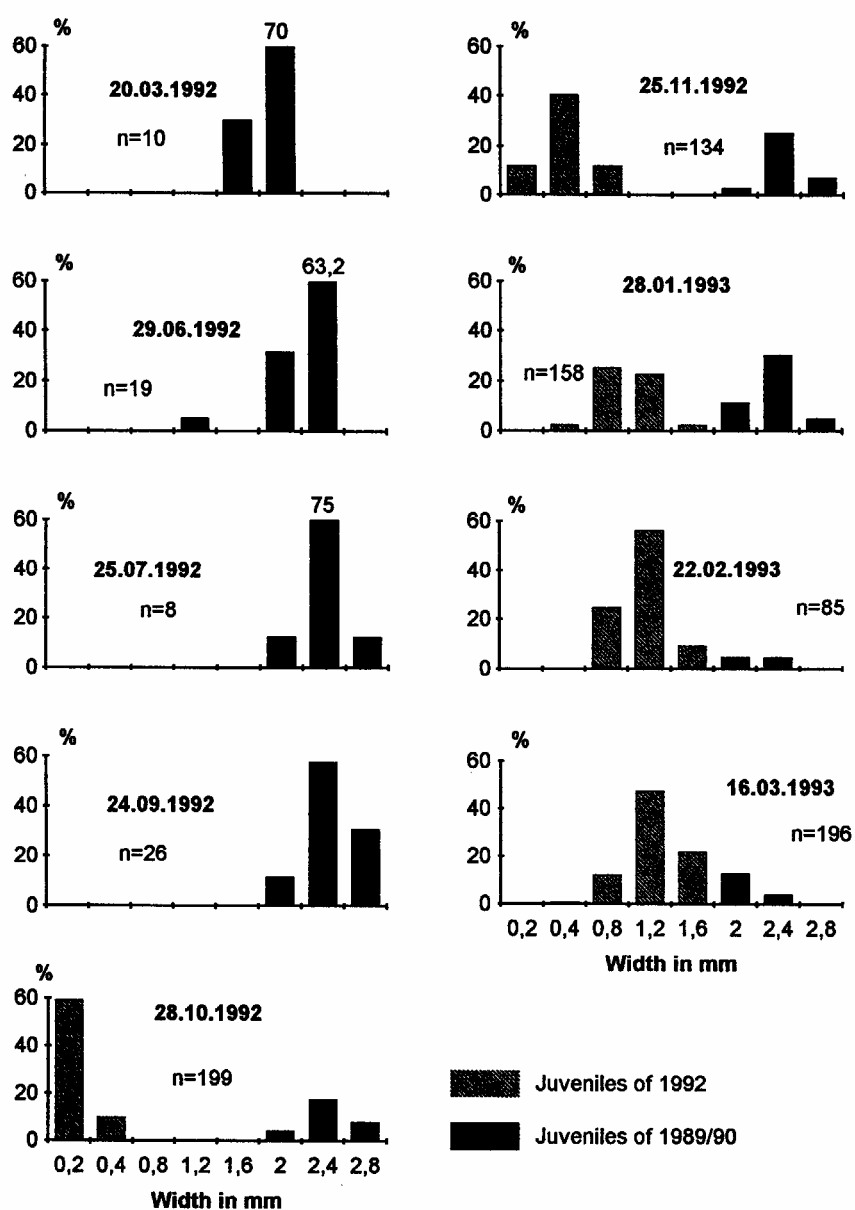


Figure 9: Size-frequency distribution of *M. viridis* at stn. 2 based on the greatest width (mm) between the 5th and 10th setiger

and different maximum widths indicate that growth rates differ between stations.

The relation between width and length or number of segments can be expressed by exponential functions (Table 2).

Table 2: Relations between the width and the length or number of segments

	relation (length-width)	r ² (coefficient of regression)	n
stn. 2	$l = 1.994 \cdot 4.507^W$	0.958	123
stn. 4	$l = 1.739 \cdot 4.645^W$	0.947	176
	relation (number of segments-width)	r ² (coefficient of regression)	n
stn. 2	$s = 16.054 \cdot 2.699^W$	0.962	123
stn. 4	$s = 16.763 \cdot 2.627^W$	0.941	76

Discussion

Since migrating into the coastal waters of the southern and central parts of the Baltic Sea, *M. viridis* has continued to spread and is now a dominant element of the local fauna (e.g. Bick et al. 1993, Zmudzinski et al. 1993). Although Webster (1879), Verrill (1873) and Essink and Kleef (1993) report that this polychaete colonizes mainly shallow waters, its range is not restricted to such regions. Holland et al. (1980), Gruszka (1991) and Zmudzinski et al. (1993) have found *M. viridis* at depths of 12 to 45 m. According to George (1966), Kinner and Maurer (1978) and Foster (1971), *M. viridis* is a euryhaline polychaete inhabiting mainly meso- to oligohaline regions and it can be considered to be a genuine brackish water species. Dörjes and Howard (1975) described a typical *Scolecoplepides* (= *Marenzelleria*) region in a stretch of the river Ogeechee where the salinity ranged from 0.2 PSU to 12.2 PSU and the spionid composed up to 85 % of the macrobenthos. Conditions were similar (S = 4 to 7 PSU) in the central part of our investigation area where abundances and wet weights were highest (4 000 to 8 000 ind · m⁻², 500 to 700 g · m⁻²) and the spionid accounted for 80 to 90 % of all macrobenthic individuals. In our region, the abundance of *M. viridis* was lower at salinities >7 PSU and <4 PSU. However, the distribution of the spionid is affected not only by salinity and perhaps competition (Levin 1982), but also by substrate affinity. Like Verrill (1873), Essink and Kleef (1988, 1993), Atkins et al. (1987) and Tourtellotte and Dauer (1983), we noted that adult animals showed a preference for sand. At stn. 6, for instance, abundances of up to 2 000 ind · m⁻² were found in a sandy bottom (1 % dw org. content, 0.86 % < 0.063 mm) at a depth of 0.5 m. In a muddy sediment (2 % dw organic content, 5.2 % < 0.063 mm) at a depth of 1.2 m just 10 m away (stn. 5) the mean abundance was only 100 ind · m⁻². Sandy bottoms also predominated at the stations where the highest abundances were found. In contrast, the muddiest bottom, highest in organic content and smallest in mean grain size were found at stn. 9 (Table 1), and it was here and at stn. 10, which represented the opposite extreme, that *M. viridis* abundances were lowest.

Biomasses increased in the central part of the bodden chain during the course of the study and *M. viridis* is continuing to spread and colonize the western part of these waters. Arndt (1991) reported wet weights of up to $82 \text{ g} \cdot \text{m}^{-2}$ in the Saaler Bodden, whereas we found values between 250 and $370 \text{ g} \cdot \text{m}^{-2}$. Gonadal maturation certainly accounts for much of the increase in biomass during the reproductive period (September to November), but migration from the western part of the bodden chain may also be involved since abundances increased as well, especially in areas with relatively high salinities. However, no simultaneous decrease in biomass and abundance was observed at stations in the western part of the bodden chain. Initial studies suggest that vertical migration takes place during the reproductive period. Dauer *et al.* (1980, 1982) reported that adult *M. viridis* caught in the plankton of the Lafayette River (Virginia, USA) were carrying ripe gonads. Adult specimens (40 - 70 mm, about 180 segments) were caught only during the reproductive period, which is in February and early March in North American coastal waters. Later catches contained only juvenile *M. viridis* (38 - 55 segments). The authors suggested that *M. viridis* experiences three planktonic phases: one serving the movement of adult animals to higher salinities, one for the release of ripe gonads and one for the transport of juveniles to lower salinities. We can confirm the motility of *M. viridis*, but found no link between swarming behaviour and reproduction. It seems probable that *M. viridis* spreads into oligohaline regions as juveniles (30 to 80 segment stage). Indeed, otherwise it would be difficult to explain the abundant and dominant presence of the species at our stns. 1 and 2, since George (1966) reported that larvae are unable to complete their development at salinities below 5 PSU.

Past descriptions of the burrows and vertical distribution of *M. viridis* appear to be inadequate, or are obviously not applicable to the region we studied. For instance, Dauer *et al.* (1981) found greatly ramified burrows in Chesapeake Bay, Virginia (North America). In the boddens *M. viridis* does not build branched burrows, but, in the top 5 cm of the sediment, may use the greatly ramified burrows of *H. diversicolor* (Zettler *et al.* 1994). Dörjes and Howard (1975) and Howard and Frey (1975) described the burrows in Ogeechee River (Georgia, USA) as being more or less unbranched, penetrating to a depth of 15 cm and having a width of 1 mm. Essink and Kleef (1988) reported vertical, unbranched burrows with a maximum depth of 30 cm and a width of 2 mm in the Dollart (Dutch North Sea coast). Atkins *et al.* (1987) found similar results in the Tay estuary in Scotland, reporting that 75 % of adult *M. viridis* were deeper than 10 cm and 35 % deeper than 20 cm. In contrast, over 90 % of the juvenile *M. viridis* and adult *H. diversicolor* were found in the top 10 cm of the sediment. Our studies show that the burrows of *M. viridis* in the bodden chain resemble those of the North Sea population. However, variations in sediment quality also have some effect. The more firmly packed or muddy the substrate, the smaller the burrows depth (Zettler *et al.* 1994). The reasons for this are probably of mechanical nature.

The reproduction period (spawning, planktonic development, settlement) of *M. viridis* populations in North America (Mead 1897, George 1966, Whitlatch 1977, Holland *et al.* 1980, Jordan and Sutton 1984) and the North Sea (Atkins *et al.* 1987, Essink and Kleef 1988, 1993) is reported to be from February to May or July. We observed that reproduction took place mainly from September to December, and the substrate was colonized by juveniles mainly in October/November. The reasons for the earlier maturation, fertilization and larval development in our region are unclear, especially since climatic conditions are similar. The North Sea and North American habitats differ from those in the Baltic only in the genuine estuarine nature of the former. They are therefore subject to tidal variations in water level and therefore specific

salinity fluctuations. Competition is more fierce than in the coastal waters along the Baltic coast (Remane and Schlieper 1971). It seems possible that so much energy is needed for the continually changing osmotic regulation that gametal maturation may be delayed in some places. In the Baltic Sea, gametal development starts in May or June, and the animals are able to spawn in October (*i.e.* before winter), whereas this process only starts in October and ceases during the winter in North American and North Sea populations (Bochert 1993). These populations therefore do not spawn until February (Atkins *et al.* 1987, Dauer *et al.* 1980, Essink and Kleef 1993, George 1966, Holland *et al.* 1980, Jordan and Sutton 1984, Mead 1897, Whitlatch 1977).

It is interesting to note that we observed the lowest abundance of *M. viridis* juveniles in the western part of the bodden chain because it was in this area that Bochert (1993) recorded the largest catch of planktonic larvae ($21.8 \cdot 106 \text{ ind} \cdot \text{m}^3$). The low abundance is obviously due to high mortality during the planktonic phase and settlement in this low salinity region. George (1966) noted that larval development ceased at salinities below 5 PSU. The relatively low abundance of juveniles in the eastern part of the bodden chain is probably due to the small number of mature adults and competition with *Hediste diversicolor*, *Corophium volutator*, *Hydrobia ventrosa* and oligochaetes (Naididae) for space and food.

The significant differences in levels of colonization by juveniles at stns. 5 and 6 may be due to a preference for sandy sediment rather than mud and the lack of competition and predation (few adult *M. viridis* and *H. diversicolor*) at stn. 5. Essink and Kleef (1988, 1993) reported that juvenile *M. viridis*, unlike adults, prefer a muddy substrate with high organic content. However, adult *M. viridis* might also have a negative intraspecific effect on the settlement of larvae and early juvenile benthic stages because Dauer *et al.* (1981), Tamaki (1985) and Levin (1982) reported that spionids negatively affect settlement of juvenile polychaetes.

Juvenile *M. viridis* were able to grow at all stations from mid-October to mid-March at temperatures between -0.5 to 4 °C. The high growth rate at stn. 2 was probably due to lack of intra- and interspecific competition, but ideal food availability may have been a contributing factor.

The presentation of width measurements in width frequency histograms shows that *M. viridis* has a life expectancy of at least two years. Two or three generations are found at the same time. Essink and Kleef (1993) also reported the co-existence of several generations and a life expectancy of more than one year. Atkins *et al.* (1987) observed that *M. viridis* did not reproduce at regular intervals. The situation in the bodden chain appeared to be similar. Although reproduction occurred in 1991, it was much lower than in the following year. However, it is almost certainly influenced strongly by salinity and temperature fluctuations (Bochert 1993). The salinity in the bodden chain was about 2 PSU higher in 1992 than in 1991, and the temperature at the beginning of October was over 10 °C, which would definitely permit better larval development.

References

- Arndt, E.A., 1988: Zusammenfassende Ergebnisse von Untersuchungen am Makrozoobenthos der Darß-Zingster Boddenkette von 1969-1987. *Wiss. Zeit. WPU Rostock, N-Reihe* 37: 6-12.
- Arndt, E.A., 1991: Long-term investigations on the macrozoobenthos in the oligohaline Saaler Bodden south of the peninsula Darß-Zingst and the invasion of *Marenzelleria viridis* in the late 80s. 12th BMB Symp., Helsingør, Denmark, p. 25-30.

- Atkins, S.M.; Jones, A.M.; Garwood, P.R., 1987: The ecology and reproductive cycle of a population of *Marenzelleria viridis* (Annelida: Polychaeta: Spionidae) in the Tay Estuary. Proc. Royal Soc. Edinburgh 92B: 311-322.
- Bick, A.; Burckhardt, R., 1989: Erstnachweis von *Marenzelleria viridis* (Polychaeta, Spionidae) für den Ostseeraum, mit einem Bestimmungsschlüssel der Spioniden der Ostsee. Mitt. Zool. Mus. Berl. 65: 237-247.
- Bick, A.; Bochert, R.; Zettler, M.L., 1993: *Marenzelleria viridis*, an invader among the benthic community in Baltic coastal inlets - distribution and reproductive strategy. 28th Europ. Mar. Biol. Symp., Crete, Greece.
- Bochert, R., 1993: Reproduktion und Larvalentwicklung von *Marenzelleria viridis* (Verrill, 1873) (Polychaeta, Spionidae) in der Darß-Zingster-Boddenkette. Dipl.-Arb., Univ. Rostock, FRG.
- Bochert, R.; Bick, A.; Zettler, M.L.; Arndt, E.A., 1993: *Marenzelleria viridis* - An invader in the benthic community of Baltic coastal inlets - Investigations of the reproduction. Proc. 13th BMB Symp., Riga, Latvia.
- Correns, M., 1976: Charakteristische morphometrische Daten der Boddenkette südlich des Darß und des Zingst. Vermessungstechnik 24: 459-461.
- Dauer, D.M.; Ewing, R.M.; Tourtellotte, G.H.; Baker, H.R., Jr., 1980: Nocturnal swimming of *Scolecopelides viridis* (Polychaeta: Spionidae). Estuaries 3: 148-149.
- Dauer, D.M.; Maybury, C.A.; Ewing, R.M., 1981: Feeding behaviour and general ecology of several spionid polychaetes from the Chesapeake Bay. J. Exp. Mar. Biol. Ecol. 54: 21-38.
- Dörjes, J.; Howard, J.D., 1975: Estuaries of the Georgia Coast, U.S.A.: Sedimentology and biology. IV. Fluvial-marine transition indicators in an estuarine environment, Ogeechee River-Ossabaw Sound. Senckenbergiana marit. 7: 137-179.
- Essink, K.; Kleef, H.L., 1988: *Marenzelleria viridis* (Verrill, 1873) (Polychaeta: Spionidae): a new record from the Ems Estuary (The Netherlands/ Federal Republic of Germany). Zool. Bijdr. 38: 1-13.
- Essink, K.; Kleef, H.L., 1993: Distribution and life cycle of the North American Spionid Polychaete *Marenzelleria viridis* (Verrill, 1873) in the Ems Estuary. Neth. J. Aquat. Ecol. 27: 237-246.
- Foster, N.M., 1971: Spionidae (Polychaeta) of the Gulf of Mexico and the Caribbean Sea. Stud. Fauna Curacao Carib. Isl. 36: 1-183.
- George, J.D., 1966: Reproduction and early development of the spionid polychaete, *Scolecopelides viridis* (Verrill). Biol. Bull. 130: 76-93.
- Gruszka, P., 1991: *Marenzelleria viridis* (Verrill, 1873) (Polychaeta: Spionidae)- a new component of shallow water benthic community in the southern Baltic. Acta Ichth. Pisc. XXI Suppl.: 57-65.
- Holland, A.F.; Mountford, N.K.; Hiegel, M.H.; Kaumeyer, K.R.; Mihursky, J.A., 1980: Influence of predation on infaunal abundance in upper Chesapeake Bay, USA. Mar. Biol. 57: 221-235.
- Howard, J.D.; Frey, R.W., 1975: Estuaries of the Georgia Coast, U.S.A.: Sedimentology and Biology. II. Regional animal-sediment characteristics of Georgia estuaries. Senckenbergiana marit. 7: 33-103.
- Jordan, R.A.; Sutton, C.E., 1984: Oligohaline benthic invertebrate communities at two Chesapeake Bay power plants. Estuaries 7: 192-212.
- Kinner, P.; Maurer, D., 1978: Polychaetous annelids of the Delaware Bay region. Fish Bull. 76: 209-224.
- Kirkegaard, J.B., 1990: Ny amerikansk havborsteorm i Ringkøbing Fjord. Flora og Fauna 96: 63-65.

- Levin, L.A., 1982: Interference interactions among tube-dwelling polychaetes in a dense infaunal assemblage. *J. Exp. Mar. Biol. Ecol.* 65: 107-119.
- Maciolek, N.J., 1984: New records and species of *Marenzelleria* Mesnil and *Scolecopides* Ehlers (Polychaeta: Spionidae) from Northeastern North America. *Linn. Soc. New South Wales*: 48-62.
- McLusky, D.S.; Hull, S.C.; Elliott, M., 1993: Variations in the intertidal and subtidal macrofauna and sediments along a salinity gradient in the upper Forth Estuary. *Neth. J. Aquat. Ecol.* 27: 101-109.
- Mead, A.D., 1897: The early development of marine annelids. *J. Morph.* 13: 227-324.
- Persson, L.-E., 1990: The national Swedish environmental monitoring programme (PMK): Soft-bottom macrofauna monitoring off the south coast of Sweden-Annual Report 1990. *Stat. Naturvardsverk, Solna, Naturvardsv. Rapp.* 3937.
- Remane, A.; Schlieper, C., 1971: *Biology of brackish water*. Stuttgart: Gustav Fischer Verlag.
- Tamaki, A., 1985: Inhibition of larval recruitment of *Armandia* sp. (Polychaeta: Opheliidae) by established adults of *Pseudopolydora paucibranchiata* (Okuda) (Polychaeta: Spionidae) on an intertidal sand flat. *J. Exp. Mar. Biol. Ecol.* 87: 67-82.
- Tourtellotte, G.H.; Dauer, D.M., 1983: Macrobenthic communities of the Lower Chesapeake Bay. II. Lynnhaven Roads, Lynnhaven Bay, Broad Bay, and Linkhorn Bay. *Int. Rev. gesamt Hydrobiol.* 68: 59-72.
- Verrill, A.E., 1873: Report upon the invertebrate animals of Vineyard Sound and the adjacent waters, with an account of the physical characters of the region. *US Comm. Fish and Fish.* Part I: 295-778.
- Webster, H.E., 1879: Annelida Chaetopoda of New Jersey. *Annual Report on the New York State Mus. Nat. Hist.* 32: 101-128.
- Whitlatch, R.B., 1977: Seasonal changes in the community structure of the macrobenthos inhabiting the intertidal sand and mud flats of Barnstable Harbor, Massachusetts. *Biol. Bull.* 152: 275-294.
- Whitlatch, R.B., 1981: Animal-sediment relationships in intertidal marine benthic habitats: Some determinants of deposit-feeding species diversity. *J. Exp. Mar. Biol. Ecol.* 53: 31-45.
- Zettler, M.L., 1993: Untersuchungen zur Biologie und Ökologie von *Marenzelleria viridis* (Polychaeta: Spionidae) in der Darß- Zingster Boddenkette. *Dipl.-Arb., Univ. Rostock, F.R.G.*
- Zettler, M.L.; Bochert, R.; Bick, A., 1994: Röhrenbau und Vertikalverteilung von *Marenzelleria viridis* (Polychaeta: Spionidae) in einem inneren Küstengewässer der südlichen Ostsee. *Rost. Meeresbiol. Beitr.* 2: 215-225.
- Zmudzinsky, L.; Chubarova, S.; Dobrowolski, Z.; Gruszka, P.; Fall, I.; Olenin, S.; Wolnomiejski, N., 1993: Expansion of the spionid polychaete *Marenzelleria viridis* in the south-eastern part of the Baltic Sea. *Proc. 13th BMB Symp., Riga, Latvia.*

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