Research Article

# PATTERNS OF SPATIAL AND TEMPORAL DISTRIBUTION OF THE *MARENZELLERIA* CF. *VIRIDIS* POPULATION IN THE LAGOON AND MARINE ENVIRONMENT IN THE SOUTHEASTERN BALTIC SEA

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## Abstract

The parameters of the dynamics of two populations of the North American polychaete *Marenzelleria* cf. *viridis* in Baltic waters were considered from the time of invasion in the Vistula Lagoon and the Russian exclusive economic zone (EEZ) in the southeastern Baltic. Both of the populations are self-reproducing and have been rather stable during recent years.

In contrast to the marine population, the one in the lagoon is characterized by high abundance, biomass, and frequency of occurrence. The differences observed are considered in relation to food supply, habitats, and inter-specific competition. Salinity fluctuations in the lagoon and food supply in the marine zone were defined as the main factors influencing the development of the populations.

## INTRODUCTION

*Marenzelleria* cf. *viridis* (Verrill 1873) has been one of the most successful and well studied alien species of the Baltic Sea during the past few decades. Some 30 papers have addressed different aspects of the biology of this species and its invasion history in the Vistula Lagoon. The occurrence and distribution of *M*. cf. *viridis* were considered in Żmudziński *et al*. 1996; Rudinskaya 1998; Ezhova 2000, and its role in bottom communities and its impact on the ecosystem in Żmudziński 1996, 2000; Ezhova & Peretertova 1999; Ezhova & Pavlenko 2001. The population development of *M*. cf. *viridis* since its introduction has not yet been reviewed, and the time is ripe for it.

There are no papers which describe the *M*. cf. *viridis* population in the coastal waters of the southeastern Baltic, and only one article (Gusev & Urbanovich 2001) regards the distribution of the youngest generation of *M*. cf. *viridis* in the Russian EEZ during autumn. Thus, the aim of the current study was to estimate and compare the characteristics of the population in the Vistula Lagoon and the coastal zone of the Baltic Sea.
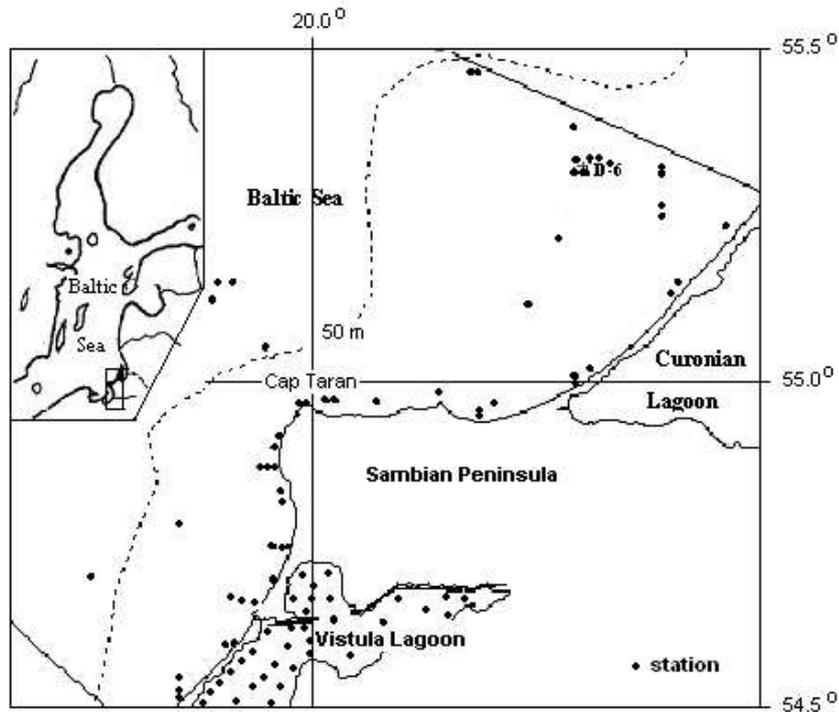


**Fig. 1.** Study area and sampling stations.

## MATERIALS AND METHODS

### *Study area*

The investigations were conducted in the northeastern (Russian) part of the Vistula Lagoon and the southeastern part of the Baltic Sea inside the Russian EEZ.

The Vistula Lagoon is a shallow, brackish water basin that is separated from the Gulf of Gdansk by the Vistula Spit (Fig.1). The total length of the lagoon is 90.7 km, and that of the eastern part is 53.6 km. The average depth is 3.1 m, and maximal depth is 5.2 m (Lazarenko & Majewski 1975).

There is a seasonal trend for salinity to increase from spring (1-3 PSU) until late fall (7.7 PSU); this is related to meteorology and wind surge. The mean annual salinity is 4-5.5 PSU (Lazarenko & Majewski 1975). The distribution of bottom sediments is typical with sandy sediments extending along the shores. These are gradually displaced by silts in the central part of the lagoon. The most frequent sediment type is fine, aleuritic mud. The content of organic carbon in the sediment fluctuates from 0.5% to 10%, at an average of 3-5% (Blazhchishin 1995). The lagoon waters are characterized by very low transparency (Secchi depth 0.3-0.7 m) and a high concentration of suspended matter (average 30.7 $mg \cdot l^{-1}$) (Chechko 2002). Primary production is at least twice higher than in the southern Baltic Sea. The average annual primary production is 303.8 $gC \cdot m^{-2} \cdot year^{-1}$ (Renk *et al.* 2001), and phytoplankton biomass can reach 26 $g \cdot m^{-2}$ (Aleksandrov 2003).

The marine shoreline of the Kaliningrad region (157 km) consists of the shores of the Sambian Peninsula, the southern part of the Curonian Lagoon, and the northern part of the Vistula Spit (Fig. 1). Salinity does not vary significantly throughout the year (from 6.5 to 7.5 PSU). Medium-grained sands prevail along the shores; gravel-boulder bottoms are located only around Cape Taran at the western extremity of the Sambian Peninsula (Boldyrev & Zinchenko 1972). Secchi depth, or water transparency, in the study area is 2-3 m, and suspended matter content fluctuates from 0.2 to 12.4 $mg \cdot l^{-1}$ (at an average of 3.3 $mg \cdot l^{-1}$). A characteristic feature of this coastal area is the current that runs along the shore mainly in a northward direction. This current transports suspended matter along the shore from 0 to 25-30 m (Boldyrev *et al.* 1979). The phytoplankton biomass in the 0 to 25 m zone ranges from 0.31 to 1.89 $g \cdot m^{-3}$. The organic matter content of the sediment is below 2% (Malicki & Miętus 1994).

### *Field data*

Samples were collected from the Vistula Lagoon monthly or seasonally during monitoring cruises (1997-2004) and during benthic studies (1998-2002)

(Table 1). During summer surveys (June, August), 40 stations were sampled in the 1998-2001 period (Fig.1). Data from the marine areas were collected during the summer (2000-2003) and autumn (2003) surveys (Table 1).

**Table 1**

The scope of analyzed benthic data.

| Water basin | Month/year | Quantity | Type of sampler | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Petersen grab | Petersen grab | Geoligical corer | Petersen grab | Geoligical corer | Petersen grab | Petersen grab | DAK-100 grab | Petersen grab | DAK-100 grab | DAK-100 grab | DAK-100 grab |
| | | | 1997 | 1998 | 1998 | 1999 | 1999 | 2000 | 2001 | 2001 | 2002 | 2002 | 2003 | 2004 |
| Vistula Lagoon | April | stations | 8 | | | | | | 7 | | | | | 6 |
| | | samples | 22 | | | | | | 21 | | | | | 27 |
| | May | stations | | 17 | | 40 | | | 9 | | | 5 | 7 | |
| | | samples | | 45 | | 120 | | | 18 | 41 | | 25 | 35 | |
| | June | stations | 13 | 14 | | | | 4 | 8 | | | 7 | | 6 |
| | | samples | 38 | 38 | | | | 12 | 21 | | | 35 | | 24 |
| | Julie | stations | 14 | 16 | | | | 39 | | | 7 | | | 7 |
| | | samples | 36 | 44 | | | | 117 | | | 4 | 18 | | 34 |
| | August | stations | 11 | 15 | | 39 | 41 | 36 | | 9 | | | 4 | |
| | | samples | 25 | 47 | | 117 | 120 | 98 | | 45 | | | 16 | |
| | September | stations | 14 | 15 | | | | | | | 8 | | | |
| | | samples | 38 | 41 | | | | | | | 24 | | | |
| | October | stations | 13 | 15 | 27 | | | 6 | | | | | | |
| | | samples | 35 | 41 | 60 | | | 18 | | | | | | |
| | November | stations | 13 | | | | | | | | | | | |
| | | samples | 37 | | | | | | | | | | | |
| | December | stations | 14 | 10 | | | | 5 | | | | | | |
| | | samples | 42 | 26 | | | | 14 | | | | | | |
| Baltic Sea | | | | | | | | Corer, by divers | | | | Ocean-50 grab | | |
| | | | | | | | | 2001 | | 2002 | | 2003 | | |
| | May | stations | | | | | | 9 | | | | 17 | | |
| | | samples | | | | | | 41 | | | | 21 | | |
| | June | stations | | | | | | | | 28 | | | | |
| | | samples | | | | | | | | 78 | | | | |
| | August | stations | | | | | | 18 | | | | | | |
| | | samples | | | | | | 50 | | | | | | |

A Petersen grab (1/40 m$^2$, three replicates per station) was used to sample in the 1997-2001 period. It is the standard, recommended tool for benthic sampling in fishery research in Russian inland waters (Salazkin *et al*. 1984). It samples the benthos in the upper 7-10 cm layer of bottom sediments (the most

accessible for fish feeding) for abundance and biomass calculation purposes. *M.* cf. *viridis* was sampled with a small geological corer (diameter 62 mm, sediment depth penetration - 55 cm, three to five replicates per station), and a DAK-100 benthic grab ($1/100$ m$^2$, sediment depth penetration  - 15-20 cm, five replicates per station).

In the sea at depths to 15 m, samples were taken by divers using small corers ($1/62$ m$^2$, sediment depth penetration - 20-25 cm, three replicates per station).  An "Ocean-50" grab was used at the deeper stations ($1/4$ m$^2$, one to two replicates per station). Generally accepted methods were applied to the samples in the laboratory (Salazkin *et al.* 1984).   The amount of material collected is presented in Table 1.

**Table 2**

The ratio between the biomass and abundance of *M. viridis* estimated by geological  corer and Petersen grab.

| Area | Type of  sediment | $N_1/N_2$ | $B_1/B_2$ |
|---|---|---|---|
| NE part of the Vistula lagoon | mud or aleurite with shells | 3,65 | 60,56 |
| E part of the Vistula lagoon | sands of different grain size | 2,76 | 20,83 |
| Primorskaya Bight | Fine aleuritic mud | 2,15 | 32,94 |
| SW part of the Vistula lagoon | Aleuro-pelitic mud | 2,11 | 60,40 |
| Central part of the Vistula lagoon | Coarse aleurite | 3,54 | 88,36 |

$N_1, B_1$ - abundance and biomass estimated by geological tube, $N_2, B_2$ – by Petersen grab

*Data analyses*

Since a high degree of bottom biotope patchiness is characteristic for the Vistula Lagoon, 40 stations were selected according to habitat diversity (Fig. 1). The spatial distribution of *M.* cf. *viridis* biomass was estimated with data from three years (1998-2000). The majority of the data were collected with a Petersen grab. Parallel sampling was also conducted in 2000 with a DAK-100 box-corer and a geological tube. These double samplings clearly demonstrated the several-fold underestimation of *M.* cf. *viridis* biomass and density when the Petersen grab was used (Table 2). In order to utilize the data obtained with the Petersen grab, transitional coefficients were used to recalculate data from 20 stations representing  all  main  types  of  bottom  biotopes.  These  coefficients  were

calculated for the abundance and biomass values obtained by the different samplers for every group of stations that had similar environmental conditions. Average annual data obtained with the Petersen grab were recalculated in consideration of the coefficients mentioned above. Table 2 presents the ratios between the abundance and the biomass obtained using different samplers depending on sediment type.

The seasonal dynamics of the *M.* cf. *viridis* population was considered from year-round (ice-cover period excluded) monitoring data from 1997-1998. With samples taken with the Petersen grab, the data correspond to the upper 7-10 cm sediment layer, which permits estimating species biomass only in that particular layer. It is known that only small and medium-sized *M.* cf. *viridis* inhabit this sediment layer (Żmudzinski 1996, Peretertova 2003), and all of the youngest generations are only represented here. Thus, the data could be used to analyze the seasonal dynamics of one-year worms. Due to this, the Petersen grab data were used without recalculation.
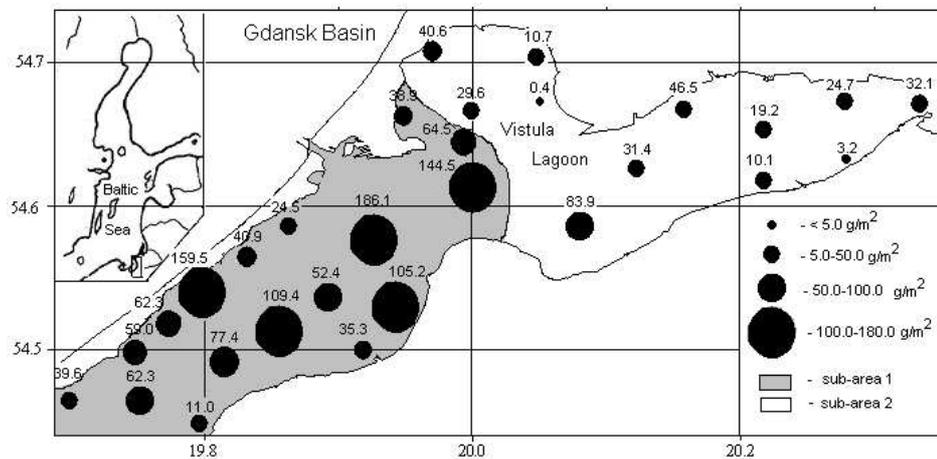


**Fig. 2.** Spatial distribution of average biomass of *M.* cf. *viridis* in the Vistula Lagoon, summer seasons from 1998 to 2000.

## RESULTS

### I. The Vistula Lagoon
#### *Occurrence and spatial distribution*

The eastern part of the lagoon can be divided into two sub-areas (Fig. 2) with different values of *M.* cf. *viridis* frequency, abundance, and biomass. In the southeastern sub-area, where inflows of sea water affect lagoon salinity, *M.* cf. *viridis* was a permanent element of the benthic community, and its frequency in
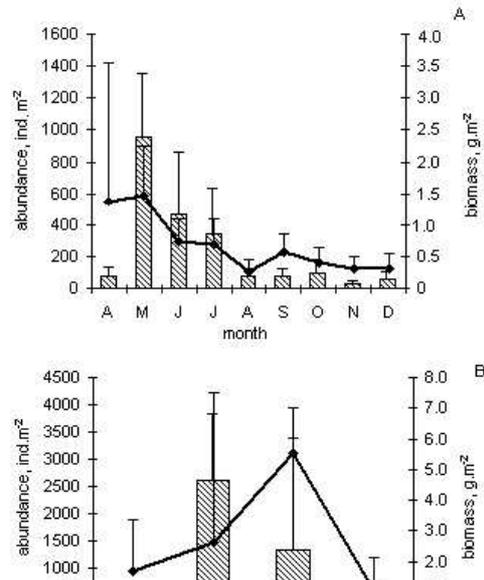
**Fig. 3.** Seasonal dynamics of abundance and biomass of *M.* cf. *viridis*.
A – Vistula Lagoon; B – Baltic Sea

samples was consistently 100% (data from 1998-1999). The average annual values of abundance and biomass in this large sub-area were $1116 \pm 345$ ind·m$^{-2}$ and $43.9 \pm 13.4$ g·m$^{-2}$, respectively. The species was present in this more saline sub-area throughout the year (Fig. 2, sub-area1).

In the innermost, northeastern part of the lagoon, which is influenced by Pregel River inflow, the frequency of the worm was only 30%. The average, annual abundance and biomass were $14 \pm 13.9$ ind·m$^{-2}$ and $0.19 \pm 0.23$ g·m$^{-2}$, respectively (Fig. 2, sub-area 2). *M.* cf. *viridis* was rather abundant here from April to June, but it disappeared completely by the end of August following a sharp decrease in its abundance in July. Thus, a permanently inhabited zone and so-called 'emigration zone', temporally occupied by a pseudo-population (Odum 1975), can be distinguished in the Vistula Lagoon (Fig. 2).

The worm produced a rather high biomass during the study period and values of about 100 g·m$^{-2}$ were usual. The highest average biomass (186 g·m$^{-2}$) was observed in the area adjacent to the Baltijsk Strait, where the highest values (423 g·m$^{-2}$) were also recorded. Low biomass of about 3.2–32.1 g·m$^{-2}$ was recorded in the polluted, freshwater region of the northeast (Fig.2).

*Seasonal and annual dynamics of biomass and abundance*
The high biomass value recorded in April when abundance is low (Fig. 3A) is evidence of the prevalence of adult individuals in the population. A sharp increase in abundance without prominent biomass changes took place in May, due to the appearance of juveniles which dominated the benthic samples during this period. Planktonic larvae occurred from September until December and

were most abundant in October (Fig.4). The highest abundance values were recorded in the central part of the study area.
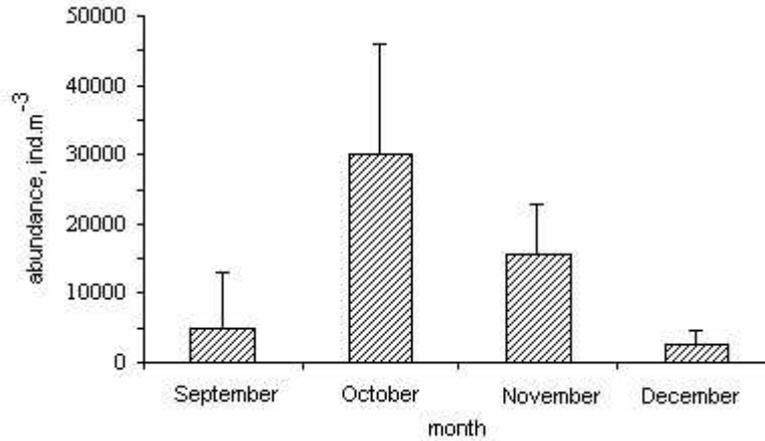


**Fig. 4.** Seasonal dynamics of *M.* cf. *viridis* larvae in the Vistula Lagoon, 1997.
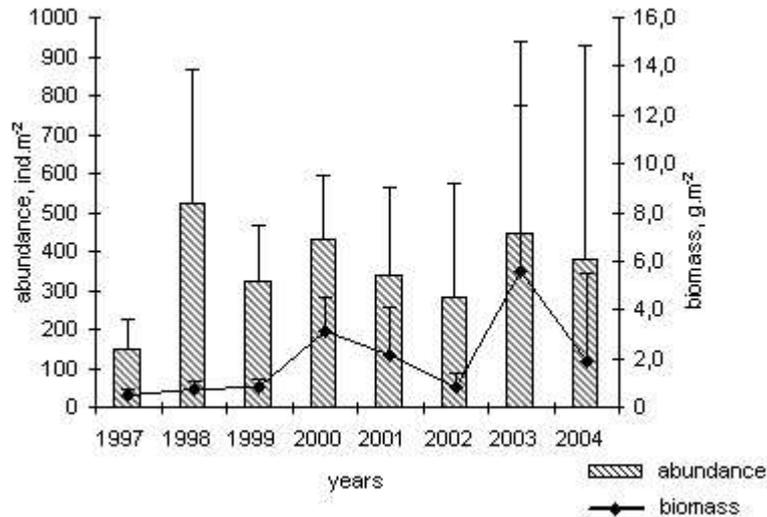


**Fig. 5.** Average annual abundance and biomass of *M.* cf. *viridis* in the Vistula Lagoon, 1997-2004.

### *Long-term changes*

During 1997-2004, the average annual abundance of *M.* cf. *viridis* in the upper 10-cm sediment layer (see Materials and Methods) ranged from 130 to 520 ind·m$^{-2}$ and biomass from 0.3 to 5.8 g·m$^{-2}$ (Fig.5). As mentioned

previously, the data collected in this period during monitoring cruises refer to the youngest generation of *M.* cf. *viridis* and do not represent the abundance/biomass of all the age-size classes. The analyses of monitoring data from 1997-2004 did not indicate any statistically valid trend of increasing or decreasing abundance or biomass and suggest a kind of stable equilibrium in the *M.* cf. *viridis* population.
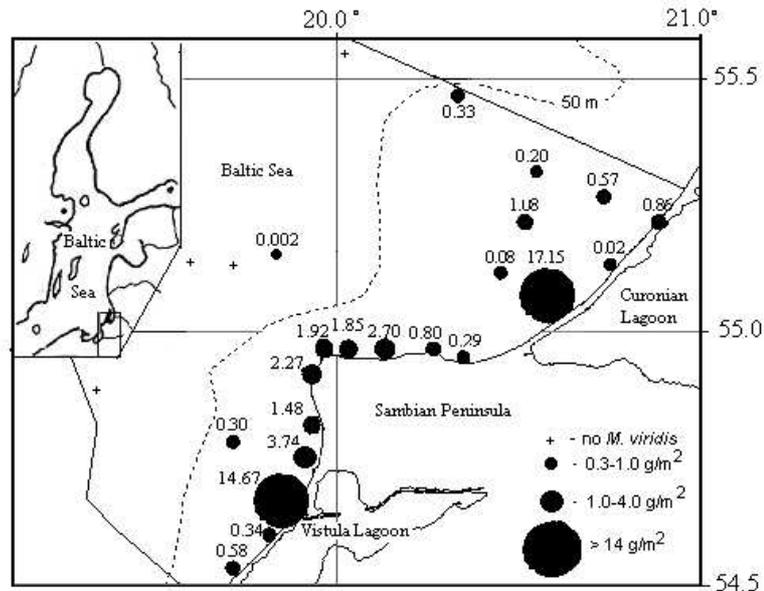


**Fig. 6.** Spatial distribution of *M.* cf. *viridis* biomass in the Russian EEZ, Baltic Sea, 2001-2003.

## II. The Baltic Sea
### *Spatial and temporal distribution*

*M.* cf. *viridis* occurred everywhere along the shore, and its frequency in benthic samples of depths up to 15 m was 100%. The variation in biomass and abundance among stations was at least ten-fold. Frequency decreased with the depth: at 20 m it was 40%, at 30 m – 20% and below 70 m the worm was not found.

Compared with the Vistula Lagoon, biomass was low in the sea at average values of only 1.7 g·m$^{-2}$. In general, the distribution of biomass along the marine shore is very uniform. Only two local maxima of *M.* cf. *viridis* biomass were observed - in proximity to the Baltijsk Strait and near the southernmost part of the Curonian Spit (Fig. 6); both were in shallow zones. Biomass values were 14.67 g·m$^{-2}$ and 17.14 g·m$^{-2}$, respectively. The worm was absent in the area near

Cape Taran, where the bottom is covered with gravel, pebbles, and boulders. However, comparatively high *M.* cf. *viridis* biomass (6.38 g·m$^{-2}$) was observed at the same region on gravel-mud bottoms.

The distribution of the abundance and biomass of *M.* cf. *viridis* along the depths was not uniform. Minimal values of abundance and biomass were recorded at depths from 0 to 5 m at an average of 542 ind·m$^{-2}$ and 1.42 g·m$^{-2}$, respectively. Between the 10 and 15 m isobaths the abundance and biomass were 3.98 - 2.58 g·m$^{-2}$ and 2621-1193 ind·m$^{-2}$, respectively. Maximal values (28.5 g·m$^{-2}$ and 21800 ind·m$^{-2}$) were observed at depths of 10 m along the shoreline throughout the area. *M.* cf. *viridis* biomass higher than 10 g·m$^{-2}$ and abundance higher than 2000 ind·m$^{-2}$ were the most frequent here. A pronounced decreasing trend in these quantitative parameters was observed below depths of 10 m (Fig. 7).
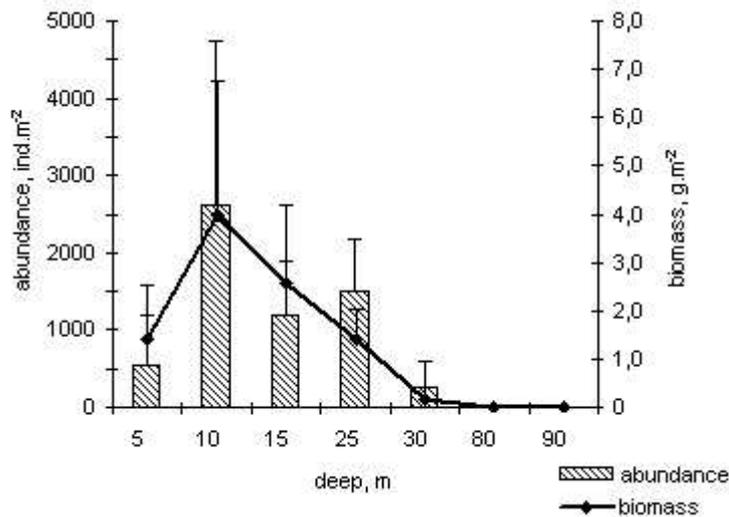


**Fig. 7.** Vertical distribution of *M.* cf. *viridis* abundance and biomass in the Russian EEZ, Baltic Sea, 2001-2003.

The peak of quantitative parameters of the population was recorded in late summer when the biomass of *M.* cf. *viridis* was three-fold and abundance even six-fold higher than in spring (Fig. 3 B). High abundance in summer is connected to recruitment, but unlike the lagoon population, the share and numbers of the youngest generation were maximal in August, not in May. Planktonic *M.* cf. *viridis* larvae were not yet present in the zooplankton samples from May.

## DISCUSSION

### *Distribution pattern*

*M.* cf. *viridis* demonstrates a high degree of environmental plasticity, inhabiting an area with very changeable environmental conditions (salinity, sediments, and food supply). Data from the literature (Kube & Powilleit 1997) indicate that *M.* cf. *viridis* is predominantly a sand-dwelling species. However, in the current study, the worm was recorded inhabiting all substrata types excluding pebble-gravel bottoms, both in the lagoon and the sea. The maximal biomass (423 g·m$^{-2}$) was recorded in sandy bottoms, but very high biomass values were also observed in other types of sediments. Thus, the distribution pattern of *M.* cf. *viridis* was more or less independent of the grain size of bottom sediments in the areas studied, and other environmental factors seem to have had a greater influence on it.

Salinity was an important factor for *M.* cf. *viridis* distribution in the area despite the euryhalinity of this species, which is thought to be capable of inhabiting zones with a salinity range of 5 – 8 PSU (Kube & Powilleit 1997). The salinity range of 1-7 PSU, which was typical for the study area, did not limit species distribution. *M.* cf. *viridis* inhabited not only waters of a salinity of 5-8 PSU, but also the zone with 1-3 PSU; however, biomass and abundance differed in these two sub-areas.

The sub-area with low (sub-area 2, Fig. 2) is an example of stressed conditions. The region with low salinity (area 2, fig. 2) is an example of stressed area - not only low values but also often and irregular changes of water salinity is typical feature of hydrology in this transition zone. Although the salinity of 1-3 PSU is within the range of salinity tolerance of adult *M.* cf. *viridis* individuals and its ripe gametes (Bochert 1997, Peretertova 2001), it is far from the optimal value of approximately 10 PSU (Bochert et al. 1996). It is also outside of the range of tolerance of its youngest developmental stages. Larvae failed to develop beyond the three-setiger stage when salinity was under 5 PSU. Thus, successful reproduction was not possible. The survival of larvae drifting from the more saline sub-area or from outside the lagoon is also problematic, and depends on the hydrological situation. Only larvae of the four-setiger stage have a chance of completing development to the benthic life mode under such difficult and unstable conditions (Bochert 1997). This may be the main reason for the low quantitative characteristics of the *M.* cf. *viridis* population in the freshwater parts of the Vistula Lagoon. It is likely that this oligohaline area represents a classical "emigration zone" (Odum 1975) for the lagoon population, where species abundance, biomass, and frequency decrease according to the distance from the "reproduction center". In the current study,

the "reproduction center" was located in the middle regions of the Russian part of the lagoon.

In general, the biomass of *M.* cf. *viridis* ranged from dozens to a hundred grams per square meter. These are extremely high values and have never before been reported for the Vistula Lagoon. Prior to the species invasion, the mean biomass of zoobenthos averaged 20-30 g·m$^{-2}$ only. The successful development of the lagoon population is supported by an excess of easily consumed organic matter. In the eutrophic lagoon, this excess is provided by the very high concentration of suspended matter, and the share of suspended organic matter can reach 50% due to high phytoplankton density. The surface bottom layer is also enriched with organic matter in easily consumable form.

The peculiarities of the distribution pattern specific for the marine area studied are as follows:
  - low biomass and abundance;
  - biomass decreased as depth increased;
  - the presence of two local distribution maxima along the shore.

The biomass of *M.* cf. *viridis* is approximately ten-fold lower in the sea than it is in the lagoon. These values were typically a few grams and never exceeded 30 g·m$^{-2}$. Similar data were reported by Zettler et al. (2002) for the Gulf of Riga and the adjacent sea waters, where *M.* cf. *viridis* abundance was five-fold lower than in the Gulf near the mouths of the Daugava and Pärnu rivers.

In the current study area, biomass maxima were only noted in the regions where there was local enrichment of suspended matter with organic components (Fig.7). The increased flocculation of suspended matter can take place due to contact between fresh and saline water masses, as occurs near the Baltijsk Strait, in municipal wastewater outflows, in areas adjacent to the port of Baltijsk, and the Zelenogradsk resort. Suspended matter is transported mainly along 10-meter isobaths, northward by the near-shore sea currents in the study area (Boldyrev *et. al.* 1979). This corresponded to the *M.* cf. *viridis* biomass maximum along the depth profile at a depth of 10 meters.

Thus, the pattern of *M.* cf. *viridis* spatial distribution was controlled mostly by salinity in the lagoon and by food availability in the sea.

### *Seasonal dynamics*

The peaks and drops (Fig. 3) observed in seasonal abundance and biomass might be explained by the life cycle. The population spawned in the Vistula Lagoon from September to December with the maximal density of pelagic larvae recorded in October. The autumn -winter spawning of *M.* cf. *viridis*, which began in September, was also recorded in the Darss-Zingst (Bochert 1997), Szczecin (Gruszka 1998), and Curonian (Daunys *et al.* 2000) lagoon

populations. Differences among these Baltic populations were observed for the duration of the spawning period, pelagic phase, and larvae settlement, which were most probably due to salinity regimes. In the Darss-Zingst Bodden Chain (DZBC), where the highest salinity was noted (up to 10 PSU), pelagic larvae generally disappeared in November. In the Szczecin Lagoon (2-3 PSU, on average), the larvae occurred in plankton until May, while in the Vistula Lagoon and the northern part of the Curonian Lagoon (5-7 PSU) they gradually disappeared in December. Bochert *et al*. (1997) found that 20°C and 10 PSU are optimal conditions for the reproduction and development of *M*. cf. *viridis,* although it may start reproduction in lower salinity levels since the adult worms as well as larvae tolerate a wide range of salinity. However, the critical threshold of four-setiger larvae is 5 PSU (Bochert *et al*. 1996).

In the oligohaline southeastern Baltic lagoons, there is a seasonal trend of increased salinity beginning in August (Lazarenko & Majewski 1975). Water salinity conditions that ensure the successful reproduction of *M*. cf. *viridis* only occur in autumn. The duration of the pelagic phase is sufficiently longer at low temperatures; it takes only four to five weeks at 20°C, five to seven weeks at 10°C, and 2.5-three months in winter at 5°C (Bochert 1997).

Thus, in the area of interest, the larvae began to settle and the appearance of benthic juveniles in the meiobenthos did not begin until the November to March period. In the macrobenthic samples, 0-group animals were observed in late spring-summer in the lagoon and marine study areas and contributed to the annual maxima of *M*. cf. *viridis* abundance (Fig. 3 A,B).

The further decrease of abundance and biomass could have been related to predator pressure. The sharp decrease in benthos biomass due to fish feeding pressure was typical for the Vistula Lagoon in mid summer (Krylova & Ten 1992). Another reason for the abundance and biomass decrease was probably due to a shift in the vertical distribution of *M*. cf. *viridis* individuals in the sediments that corresponded to the growth of the worms. As mentioned above, mid and large-sized *M*. cf. *viridis* individuals can penetrate sediments deeper than 10-15 cm (Żmudzinski 1996, Peretertova 2003) and only some of them could be caught with the Petersen's grab. Thus, the autumn decreases in abundance and biomass (Fig. 3A) primarily reflected the transition of the youngest generations to the elder age-size group and, thus, into deeper layers of the sediment.

### *Long-term changes*
The first records of *M*. cf. *viridis* in the Vistula Lagoon date to 1988, since by 1989 the species was observed throughout the lagoon area (Żmudzinski *et al*. 1996, Rudinskaya 1998).  The history of the invasion can be divided into four

stages:

1. Initial phase - 1988 - 1991. It was first observed outside the lagoon, near the sea entrance in 1988 and in the northeastern and northwestern lagoon areas in 1989-1990. Abundance was about 100 ind·m$^{-2}$ and biomass was 0.08 g·m$^{-2}$ (Żmudzinski *et al*. 1996, Rudinskaja 1998).

2. Exponential increase of the population - 1992-1994. Dense settlements existed in the estuarine part of the Pregel River in the summer of 1992 (Shibaeva & Potrebich 1994). Abundance was 1000-1500 ind·m$^{-2}$ and biomass was 9.0-11.0 g·m$^{-2}$. In the lagoon, the average abundance reached 5000-7000 ind·m$^{-2}$ (Żmudzinski *et al*. 1996) and the maximal was 12000 ind·m$^{-2}$ (Shibaeva & Potrebich 1994).

3. Decrease of abundance and biomass - 1995-1996. *M*. cf. *viridis* settlements disappeared in most of the freshwater areas (the river and the northeastern part of the lagoon). The species only occurred seasonally in these areas. Abundance did not exceed 3000 ind·m$^{-2}$.

4. Stable population - 1997-2004. *M*. cf. *viridis* inhabited the whole lagoon, but in the northeastern part it was usually only present from early spring until late summer. The average abundance varied from 1100 to 3000 ind.·m$^{-2}$; the frequency of occurrence was 97%, and the biomass share ranged from 5% to 75% of the total benthos in different parts of the lagoon.

Ezhova & Peretertova (1999) established that there were four distinct stages in the history of the *M*. cf. *viridis* population in the Vistula Lagoon – the initial invasion, exponential population growth, the decline phase, and the stable population phase. The data considered above indicate that the stable population phase or the "phase of stable equilibrium density" (Zettler *et al*. 2002) has been characteristic for both *M*. cf. *viridis* populations (lagoon and marine) until now. The same developmental phase was observed in the Darss-Zingst population (Zettler *et al*. 2002). There are no reliable arguments to explain the current phase of population decline. It seems that for 16 years, following a sharp initial increase and then decline, both populations have reached the quantitative parameters that provide optimal levels of food availability and inter- and intra-species competition that correspond to ecosystem capacity.

The inter-species competition for food and space was a very important factor that influenced the success of the *M*. cf. *viridis* introduction in the Vistula Lagoon and Kaliningrad seawaters. Kotta et al. (2001) noted that the bivalve *Macoma balthica* caused significant mortality among *M*. cf. *viridis* due to food competition. In the Vistula Lagoon, no suspension-feeders were abundant before the *M*. cf. *viridis* invasion. On the contrary, the two species that actively feed on seston, *M. balthica* and *M. edulis*, dominated in the marine part of the study area. It was demonstrated that *M*. cf. *viridis* should prevail only in bottom

communities where competitive interactions with these two bivalves are excluded (Zettler *et al.* 2002). Thus, in the Vistula Lagoon the situation is much more favorable for the worm, not only due to environmental conditions but also due to competitive interactions.

## CONCLUSIONS

- Both *M.* cf. *viridis* populations are self-reproducing and have been rather stable in recent years and do not exhibit a tendency to decline.
- The lagoon environment provides much more favorable conditions with regard to food supply, habitats, level of inter-specific competition, and support a ten-fold higher level of *M.* cf. *viridis* biomass than does the sea.
- The populations of *M.* cf. *viridis* are controlled by fluctuations of salinity in the lagoon and by food conditions in marine waters.

## ACKNOWLEDGEMENTS

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