

HISTORY AND SUCCESS OF AN INVASION INTO THE BALTIC SEA: THE POLYCHAETE *MARENZELLERIA* CF. *VIRIDIS*, DEVELOPMENT AND STRATEGIES

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Abstract

In the mid 1980s, a new polychaete appeared in coastal waters of the Baltic Sea and rapidly became an important faunistic element. The identification of this spionid as *Marenzelleria* cf. *viridis* indicated North America as the most likely area of origin. The history of invasion into the Baltic Sea is outlined. Sound taxonomic experience and competence was and is necessary to elucidate the background when dealing with bioinvasions. A review of taxonomic problems of the genus *Marenzelleria* is given. Based on long time series we could draw a picture on the species strategy in stressed habitats. Three coastal areas were selected to demonstrate the role of environmental factors facilitating *Marenzelleria* invasion in the Baltic Sea in the last decade. This review deals with the expansion and niching of an allochthonous species and its influence on the indigenous macrozoobenthos. Both the life history and physiology of *Marenzelleria* make it well adapted to life in brackish water conditions, occupying a niche in an environment with low species diversity.

1 Introduction and invasion history

In the late 1970s and early 1980s, a new polychaete appeared in brackish waters of the North and Baltic Seas and rapidly became an important faunistic element. Identification of this spionid was beset with problems from the start. First it was identified as *Marenzelleria wireni*, later as *M. viridis*, until genetic studies revealed differences between populations from the North Sea and the Baltic Sea and the species were named as *M. cf. wireni* (North Sea) and *M. cf. viridis* (Baltic Sea and Elbe Estuary) (Bick & Zettler 1997). The identification of the Baltic species as *Marenzelleria* cf. *viridis* led justifiably to assume that it had very probably been introduced from North America. Genetic studies showed the correspondence with animals from the Arctic (Canada) and several coastal waters along U.S. coast (New Hampshire to Georgia) (Bastrop et al. 1997).

M. cf. viridis prefers oligo- to mesohaline conditions. The species colonizes soft bottom habitats and inhabits vertical mucus-lined burrows down to sediment depths of 35 cm. The species reaches a size up to 120 mm in length (250 setigers) and has a life span of approximately 3 years (Zettler 1996b, 1997a). Fertilized eggs occur in the water column and the larval development is entirely pelagic for 4-12 weeks (Bochert 1997).

The way of introduction into the Baltic is not fully clear yet. The transport as larvae in the ballast water is likely. The enormous production of larvae is probably the reason for the rapid speed of dispersal. The species was probably first introduced to the harbors of

Swinoujście or Stralsund (Gruszka 1999). In 1985 *M. viridis* was first reported from the Baltic Sea in a German coastal water (Bick & Burckhardt 1989). Since then the species spread effectively and established practically along all coasts of the Baltic to the Åland Islands, the Gulf of Finland, the Gulf of Riga and the Bothnian Bay (Fig. 1).

In 1986 *Marenzelleria* was observed in Polish waters (Gruszka 1991; Maslowski 1992) and in 1988/89 it reached Lithuanian, Latvian and Estonian waters (Olenin & Chubarova 1992; Lagzdins & Pallo 1994; Zmudzinski et al. 1997; Kotta & Kotta 1998). In the beginning of the 1990s the species occupied Swedish and Finnish coastal areas (Persson 1990; Stigzelius et al. 1997). By the early 1990s *M. viridis* managed to colonize almost the whole Baltic Sea. At the end of the century the polychaete found its way into the northernmost part of the Baltic, the Bothnian Bay (Leonardsson 2001). Recently the highest densities ($> 5,000$ ind m^{-2}) of *M. viridis* were observed in the south-western part of the Baltic (Darss-Zingst Bodden, Greifswalder Bodden, Oderhaff) (own observations) and in the Gulf of Riga (Cederwall et al. 1999) (Fig. 1). Medium abundances (500-5,000 ind m^{-2}) occur in the Bothnian Bay (Umeå area) and Vistula Lagoon (Zmudzinski et al. 1997; Leonardsson 2001). All other Baltic waters are colonized in low abundances from some few specimen to 500 ind m^{-2} (e.g. Kube et al. 1996; Boström & Bonsdorff 2000; Daunys et al. 2000).

M. viridis belongs to the most successful recent invasion species of the Baltic Sea. In the last decade this polychaete has become a dominant element (in respect to abundance and biomass) in the local zoobenthic communities of several coastal waters. This study deals with the expansion and niching of an allochthonous species and its influence on the indigenous macrozoobenthos.

2 The systematic state of *Marenzelleria*

During an investigation on the conditions of the sea fisheries of the south coast of New England (northeast coast of North America) two species of *Scolecoplepis* were recorded by Verrill in 1873: *Scolecoplepis viridis* and *S. tenuis*. Both species occurred on sandy shores of the bays and sounds in large abundance (Verrill 1873). In the beginning of the 20th century two further species, important in this context, were described from the Arctic region by Augener (1913) and Chamberlin (1920): *Marenzelleria wireni* and *Scolecoplepides arctius*.

Maciolek (1984) revised the genera *Marenzelleria* and *Scolecoplepides*. As we know now, she was wrong in some details. These mistakes were one cause of following uncertainty about the taxonomic state of specimens recorded in European coastal waters at the end of the 1970s. She transferred *S. viridis* to *Marenzelleria* and synonymised *S. tenuis* with *S. viridis* (= *M. viridis*). Maciolek described a third *Marenzelleria* species, *M. johnesi* (according to Rodi & Dauer (1996a) junior synonym of *M. viridis* and for that reason not further regarded here). As a result of this revision only two species are recognized as belonging to *Marenzelleria*: *M. wireni*, occurring in waters around the Arctic Circle, and *M. viridis*, occurring in the coastal water of the east coast of North America. According to Maciolek, *M. wireni* differs only lightly from *M. viridis*.

The occurrence of *Marenzelleria* in European coastal waters resulted in numerous ecological and taxonomical investigations. Finally the immigrant was identified as *M. viri-*

dis (Fig. 2) on the basis of Maciolek's revision and the assumed area of distribution (Atkins et al. 1987; Bick & Burckhardt 1989).

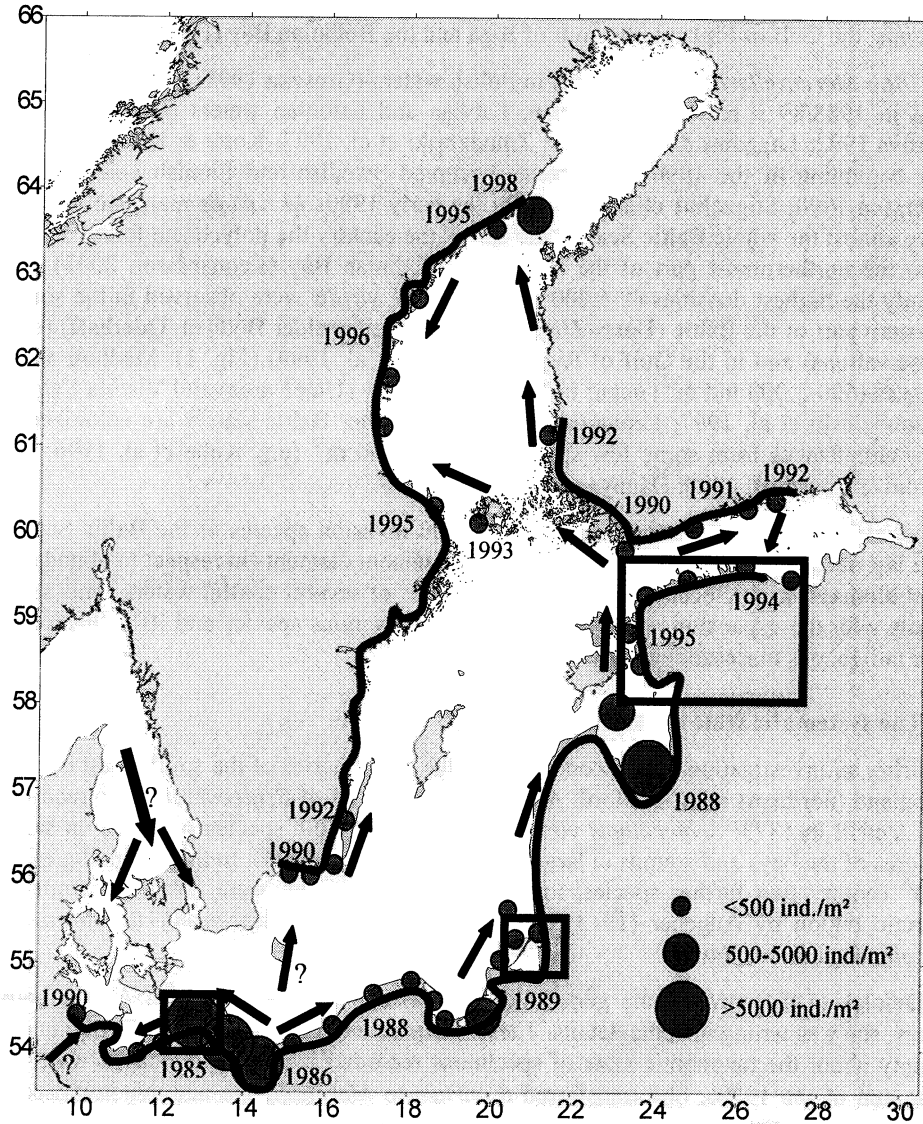


Figure 1. Invasion history of *Marenzelleria cf. viridis* in the Baltic Sea. The bold line indicates the recent distribution. The size of the circles correlates with the mean abundance recorded in the sub-areas. For data see Zettler (1997b) and references. The frames show the locations of the reference areas (from left to right: Darss-Zingst Bodden, Curonian Lagoon, Estonian waters).

Population genetic studies by Bastrop et al. (1995) showed the presence of genetically distinct forms in the North and Baltic Sea as well as in different regions of the north-

eastern coast of America. The morphological studies undertaken against this background allowed good discrimination between these species. Most important diagnostic characters are: length of nuchal organ, number of branchiate setigers and the first appearance of hooded hooks (Bick & Zettler 1997). These characters vary with growth and make it more difficult to identify juvenile worms (Bick 1995). Owing to the lack or poor condition of type material the specimens were named as *M. cf. wireni* and *M. cf. viridis*, according to Maciolek's description (Bick & Zettler 1997).

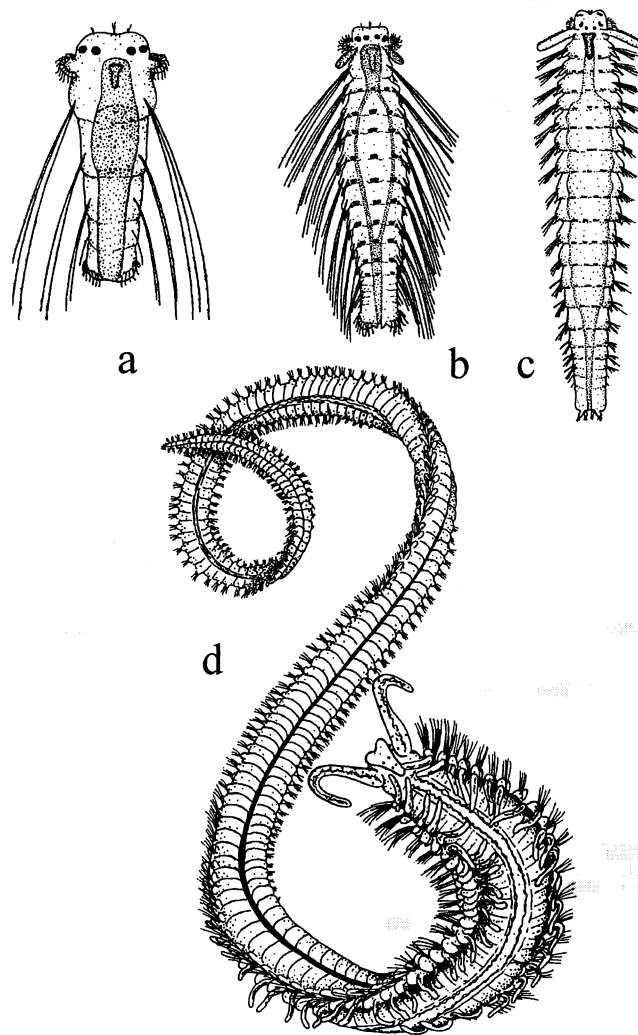


Figure 2. *Marenzelleria cf. viridis*, (a) 4-setiger larvae, (b) 15-setiger larvae, (c) juvenile benthic stage, (d) habitus of an adult worm [a-c] from Bochert & Bick (1995), (d) from Bick (1995).

In 1998, Russian polychaetologists examined types of *Scolecoplepides arctius* Chamberlin and *Laonice annenkovae* Zachs, 1925 (Sikorski & Bushinskaya 1998). They synonymised both species and suggested *S. arctius* (valid name: *M. arctia*) to be separate from *M. viridis* and *M. wireni*. According to these authors four species of *Marenzelleria* exist of which two occur in the Arctic (*M. wireni* and *M. arctia*) whereas the other could be found in coastal waters of North America and Europe (*M. johnesi* and *M. viridis*).

According to Bastrop et al. (1997) and Bick & Zettler (1997) at least three species have been found in North America, in the North Sea and in the Baltic. This means that we know 5 valid species of *Marenzelleria*, however, usage of corresponding species names is not absolutely clear. To resolve this problem, a revision with material from Arctic and boreal zones, as well as available type material (including Verrill's rediscovered material), is in preparation (Sikorski et al.).

3 Life strategies in different waters of the Baltic

M. viridis has been studied intensively since it was discovered that it has become an important component of the coastal macrozoobenthos of the Baltic Sea. Field studies and laboratory investigations have been carried out to analyse the life cycle (e.g. Bochert & Bick 1995; Bochert 1997), the distribution and physiological capacities according to ecological factors (e.g. Kube et al. 1996; Bochert et al. 1997; Burckhardt et al. 1997; Schiedek 1997; Stigzelius et al. 1997; Zettler 1997a; Zmudzinski et al. 1997; Cederwall et al. 1999; Daunys et al. 2000) and morphological and genetic features (e.g. Bastrop et al. 1997; Bick & Zettler 1997). *M. cf. viridis* was discovered in a wide range of brackish habitats, where it showed different modes of establishment. Environmental tolerance, high genetic variability, short generation time, early sexual maturity, high reproductive capacity and a broad diet are among attributes of *M. viridis*.

Three coastal areas were selected in the Baltic to demonstrate the role of environmental factors facilitating species invasion. Darss-Zingst Bodden might be characterized by favourable habitat features which benefited species establishment in the past. In contrast, both Curonian Lagoon and the Gulf of Finland/Gulf of Riga can serve as examples of stressed areas, where the species meets the limits of its environmental tolerance.

3.1 GERMAN COASTAL WATERS (DARSS-ZINGST BODDEN)

Since 1985 *M. viridis* dispersed rapidly throughout the boddens south of Darss-Zingst and became one of the dominant faunistic elements (Zettler 1996a). It has colonized a range of habitats varying from almost limnic (0.5 PSU) to brackish water regions up to 10 PSU. The brackish eutrophicated environment of the Darss-Zingst Bodden has provided excellent opportunities for the species to quickly develop a dominant population within few years (Fig. 3).

Since the first appearance of *M. viridis* in the mid 1980s, its abundance has steadily increased rising from a few hundred ind m⁻² to about 10,000 ind m⁻² in 1994. Maximum densities were revealed in the middle of the bodden (about 28,000 ind m⁻², 30-40 g AFDW m⁻²). Afterwards the densities of the spionid did strongly decrease to approx. 100 ind m⁻² in the innermost area (salinity < 3 PSU in the last 5 years) and to medium abundance of 3,000 ind m⁻² in the outer region (never < 5 PSU). A very similar devel-

opment was observed in the Dollart (The Netherlands) of the sibling species *M. wireni* by Essink & Dekker (2000). They discussed three phases of population development: an initial increase, a stabilization period and a period of decline. The developmental stages of Darss-Zingst populations are kinds of stable equilibrium density (high salinity area) and an example of an extremely stressed one (low salinity area). Due to the high variability of recruitment success, caused by high or low salinity extremes and variations of nutrition supply (sensu Bochert 1997; Burckhardt et al. 1997) in this transition area, the abundance of *M. viridis* fluctuated or decreased.

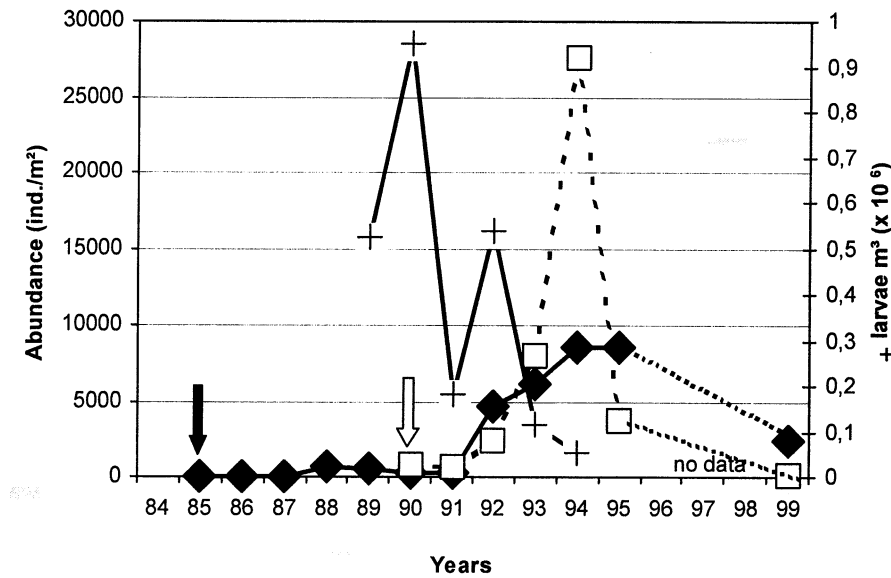


Figure 3. Mean annual abundance of *Marenzelleria* cf. *viridis* in two different (salinity) sub-areas of the Darss-Zingst Bodden from 1984 to 1999. The abundance of larvae (+) are averaged (Bochert 1997). The arrows indicate the beginning of colonization.

In the Darss-Zingst Bodden *M. viridis* occurred at greater sediment depths than other species in this area. In respect to that and in view of its rapid increase in terms of both abundance and biomass, a negative impact on the indigenous fauna was expected. In contrast the sibling species (*M. wireni*), studied in North Sea estuaries (Atkins et al. 1987; Essink & Dekker 2000), where partly drastic changes of benthic colonization were observed, comparison with pre-invasion data for Darss-Zingst Bodden revealed no negative consequences. On the contrary, colonization of the substrate by the spionid appears to encourage the proliferation of other organisms. With increasing spionid abundance an increase of most indigenous species (e.g. the polychaete *Hediste diversicolor*, chironomid larvae and hydrobid gastropods) was observed. Only the amphipod *Corophium volutator* showed a negative correlation with *M. viridis*. Several experiments (predation and competition) substantiated these results.

The lower limit of 5 PSU for successful development (metamorphosis) of *M. viridis* larvae (Bochert 1997) and the strong dependency on both food concentration and quality (Kube et al. 1996; Burckhardt et al. 1997) clarify the adaptation to eutrophic conditions prevailing in brackish waters.

3.2 LITHUANIAN COASTAL WATERS (CURONIAN LAGOON)

The benthic population of *M. viridis* also successfully established in the shallow eutrophicated Curonian Lagoon since it was first observed there in 1990 (Olenin & Chubarova 1992). The species colonized the oligohaline lagoon areas (down to mean annual salinity of 0.2 PSU) being affected by seawater inflows and does not penetrate further into permanently freshwater habitats. As in many other estuaries or lagoons of the Baltic, the species established in sandy/muddy habitats previously occupied by poor communities of oligochaetes and chironomids. Even with low densities, usually $< 500 \text{ ind m}^{-2}$, the species increased to total benthic biomass of a few 100 g m^{-2} (wet weight).

Curonian Lagoon differs from many enclosed water bodies in the Baltic by wind driven irregular salinity fluctuations during autumn and winter months. Salinity is frequently varying from freshwater up to 7 PSU at the time scale of hours to few days. The species spawning and development of pelagic larvae, which take place during cold period in the Baltic, are critical stages in *M. viridis* life history. Oosorption of ripe gametes in *M. viridis*, a typical phenomenon in the lagoon benthic population, is most likely caused by accidental salinity drops. Nevertheless, the density of pelagic stages during reproduction season may occasionally reach up to $50,000 \text{ ind m}^{-3}$ in lagoon waters. The outbursts of *M. viridis* in the Curonian Lagoon plankton community are strongly related to the seawater inflows, whereas the pelagic larvae became completely extinct under freshwater runoff conditions (Fig. 4). Lecitotrophic stages (eggs to 3-setigers) usually are most abundant among larvae contributing at least to 60% of their total density found in the plankton. In opposite, late planktotrophic stages, which are well towards metamorphosis to benthic life mode, are exceptionally rare. Development boundary at the 10-segment stage was found to be characteristic for the pelagic larvae in the lagoon waters during three years of observations (Fig. 4).

The population outside the entrance of the lagoon obviously acts as a pool of recruits: a part of its offspring is directed to the maintenance of populations in the adjacent oligohaline habitats. According to the structure of the pelagic stages, only 0.1-1.0% of those larvae that potentially "visited" the lagoon underwent metamorphosis to benthic juveniles. This recruitment is negligible compared to the average density of some few hundreds of ind m^{-2} being found in the lagoon benthic population. It is more likely that migration of juveniles during post-reproductive periods contributes more significantly to population maintenance. Migration capability of *M. cf. viridis* juveniles, reported for the Atlantic coast of North America was confirmed in the Baltic, too (see Zettler 1997b for references). Probably this mode of dispersal ensures the permanent existence of local populations for a decade since its invasion. This also coincides with steady deficiency of early benthic stages among bottom macrofauna in post-reproduction seasons.

The continuous turnover of age classes is of exceptional importance for a long-lasting establishment of species with relatively short life span. It seems that the ecological

roulette principle (Carlton & Geller 1993) fits perfectly to *M. viridis* survival and establishment in extremely stressed habitats as well.

3.3 ESTONIAN COASTAL WATERS (GULF OF FINLAND/GULF OF RIGA)

The first observation of *M. viridis* at the northern coast of the Gulf of Finland was made in 1990 (Stigzelius et al. 1997). During 1990-1993 *M. viridis* expanded its distribution into the eastern parts of the Gulf (Stigzelius et al. 1997). However, anti-clockwise circulation of the currents would not permit *M. viridis* to spread from the northern side of the Gulf towards its southern side. In addition, the larvae of the polychaete are unable to complete their development at salinities < 5 PSU (Bochert 1997), which may frequently occur in the easternmost part of the Gulf of Finland. Only one specimen was recorded in the south-eastern coast of the Gulf of Finland in 1994. Until 1997 this species was not observed along the southern coast of the Gulf. Some occasional findings of *M. viridis* in the westernmost bays suggest the Väinameri (NW Estonia) as a donor region. *M. viridis* is expanding its distribution range towards the eastern parts of the Gulf of Finland, being established as far as in Narva Bay (NE Estonia) (Kotta 2000).

Depth did not correlate with the abundance and biomass of *M. cf. viridis* while sediment type was a significant factor for both. In shallower areas (< 10 m) the species preferred sand or gravel bottoms. Deeper down (> 10 m) it was confined to silty clay bottoms (Kotta & Kotta 1998). In the more eutrophicated regions of the Gulf of Riga, i.e. off the mouths of Daugava and Pärnu rivers, the densities of *M. cf. viridis* were fivefold higher than in adjacent sea areas. Besides nutrient concentrations, higher salinity values increased the population densities of *M. viridis* in these areas.

M. viridis is a deposit-feeder sharing the same food resources with the majority of the native benthic invertebrates. Hence, the addition of *M. viridis* into the benthic system of the northern Baltic is likely to offset a stress on the native fauna due to possible competitive interactions for food and/or for space. There exists circumstantial evidence that after the invasion of *M. viridis* the densities of the polychaete *Hediste diversicolor* (Kotta & Kotta 1998) and the deep-water amphipod *Monoporeia affinis* dropped considerably in the northern Baltic Sea (Cerderwall et al. 1999). Manipulative experimental studies have demonstrated that *M. viridis* has a significant effect on the growth of *M. affinis* (Kotta 2000). The reduction in the growth of amphipods due to the competitive interaction between these species is expected to change the duration of amphipod life cycle: its recruitment is prolonged and fecundity is reduced. In the shallower areas *M. viridis* reduced the survival of *H. diversicolor*. On the other hand, the bivalve *Macoma balthica* caused a significant mortality of *M. viridis*. We suggest that the availability of food limits the population growth of *M. viridis* in the deeper parts whereas competitive interactions between *M. viridis* and *M. balthica* are a possible key factor determining the distribution pattern and abundance of *M. viridis* in the shallower parts of the northern Baltic Sea. *M. viridis* should prevail only in these biotopes where the polychaete can escape from the competitive interactions with *M. balthica*. These are for example the sea-areas adjacent to river mouths and municipal wastewater outflows where the food for deposit feeders is in excess.

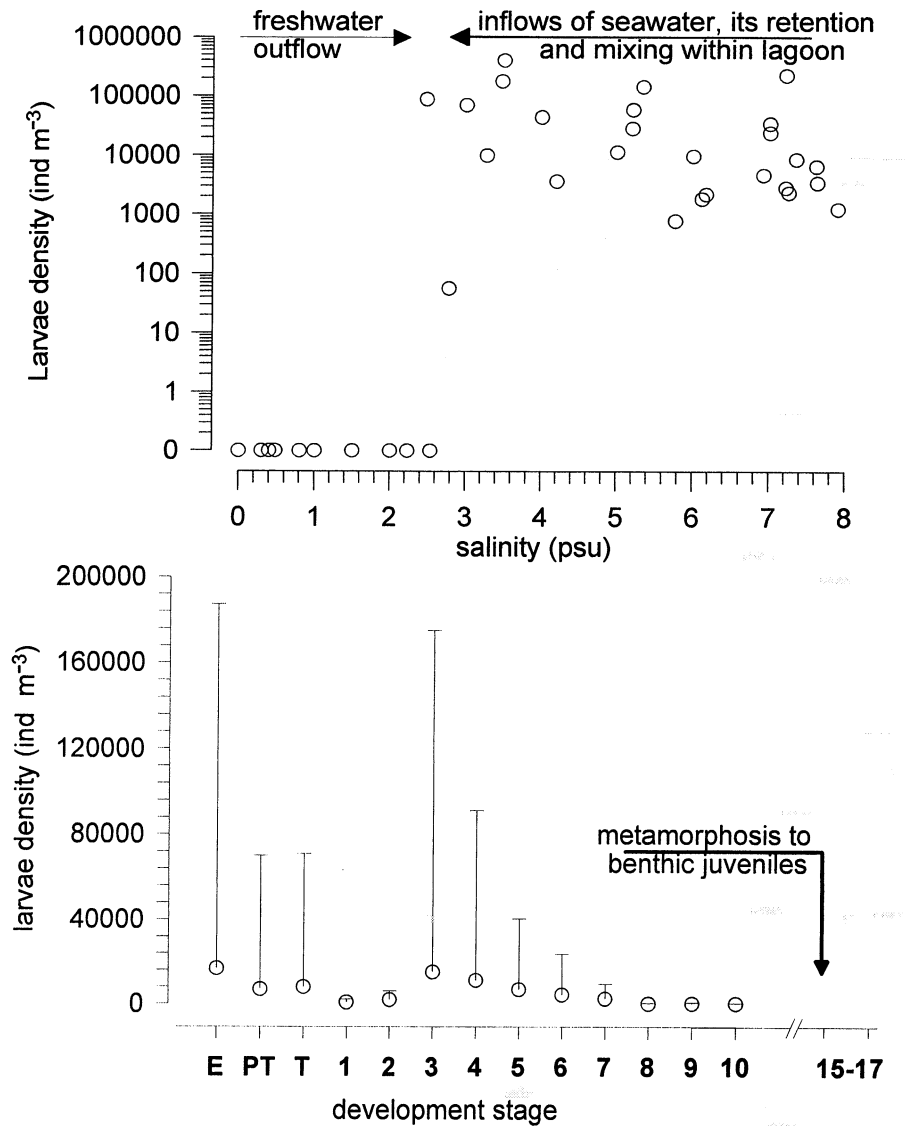


Figure 4. Density of *Marenzelleria* cf. *viridis* pelagic larvae versus salinity (top: temperature range 3-15 °C) and contribution of different development stages (bottom: averages and max. reached) to the total species abundance found in the Curonian lagoon in 1996-1999. ((E) eggs, (PT) pre-trochophores, (T) trochophores; numbers indicate stage of larvae according to the number of setigers).

4 Conclusions

Due to eutrophication, primary production is extraordinary high in most estuaries, inhabited by *Marenzelleria*. Thus, food shortage will not limit the phytoplankton feeding sponiid because of the nearly absence of filter-feeding bivalves in these horohaline

waters. In these areas with low species diversity no or weak indications on interspecific competition were observed. Moreover, positive correlations were found between densities of the new invader and local (native) species. Competition for food with the indigenous fauna is likely to occur in oligohaline waters with freshwater mussel beds (e.g. Oder Lagoon) or in more oligotrophic offshore waters with high densities of filter-feeding bivalves, like *Mytilus edulis*, *Macoma balthica* and *Mya arenaria* (e.g. Pomeranian Bay, off-shore waters) where the species exploits the same and limited food resource.

The results obtained in studies referred to in this review indicate an extremely high tolerance of the *M. viridis* adults to many environmental factors such as depth, salinity, temperature, eutrophication and sediment quality. *M. viridis* shows a Baltic wide distribution within favourable habitats in near coastal areas. It propagated in semi-enclosed shallow lagoons as well as in coastal zones and off-shore bays. Most success was observed in enclosed coastal areas, like boddens and lagoons. The success of its establishment is probably facilitated by higher summer temperature, homogeneity of habitat and eutrophication in coastal areas of the Baltic Sea. However, spawning event and development of pelagic stages were found to be critical phases in the species life cycle in stressed environments. Most likely the species is limited by salinity fluctuations rather than its average value.

Long lived though less tolerant pelagic larvae, being the species advantage to disperse over extended distances, do not ensure expansion into stressed (marginal) habitats. The key force driving the species expansion into adverse environments might be dispersal of relatively more tolerant benthic stages. However, this way of population maintenance leads to the accidental nature of the species dynamics (ecological roulette) in stressed habitats.