

Dynamics of *Marenzelleria viridis* (Polychaeta: Spionidae) pelagic larvae in Pärnu Bay, NE Gulf of Riga, in 1991–99

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Abstract. *Marenzelleria viridis*, a polychaete species originating from North America, was found in the Baltic Sea in 1985 and in the Gulf of Riga in 1988. In Pärnu Bay, the NE Gulf of Riga, pelagic larvae of *Marenzelleria* were first discovered in 1991 and have since then been annually present in the plankton community. The abundance of larvae remained relatively constant during the first 6 years, but increased abruptly in 1998–99. This interval between the recording of the first larvae and mass development of the species is extraordinarily long for the Baltic, and was possibly caused by the low salinity of Pärnu Bay. In the North and Baltic seas, two sibling species of *Marenzelleria* have been identified. The North Sea form, *M. cf. wireni*, breeds in spring, while the Baltic Sea form, *M. cf. viridis*, has only been reported to breed in autumn. In Pärnu Bay, fertilized eggs and trochophores of *Marenzelleria* occurred in plankton both in spring and in autumn, which raises a question of the identification of the spring larvae. Earlier genetic analyses have however indicated that only *M. cf. viridis* is found in the Gulf of Riga. Therefore the species is, in suitable environmental conditions, capable of reproducing two times a year. The spawning season of the Baltic *M. cf. viridis* is thus not genetically determined, but is caused by exogenous factors, such as temperature and possibly also food conditions.

Key words: *Marenzelleria viridis*, introduced species, reproduction, pelagic larvae, Gulf of Riga, Baltic Sea.

INTRODUCTION

Unintentional introductions of coastal marine species to new environments have increased during the past few decades, mainly due to increasing maritime traffic. The Baltic Sea is especially receptive to invasions since it is shallow and is characterized by various coastal habitats – archipelagoes, estuaries, bays, and

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semi-enclosed lagoons – as well as different bottom types, from mud, sand, and gravel to rocky shores. In addition, the high productivity, low salinities (mainly below 7 PSU), and relatively high summer temperatures make the Baltic prone to newcomers from estuaries and coastal seas of the world. Also, due to the short age of its present brackish-water stage, the post-glacial recolonization of the Baltic Sea by benthic species is probably still going on (Leppäkoski, 1984, 1991).

Well-known examples of nonindigenous invertebrate species in the Baltic include the soft-shelled clam *Mya arenaria* (introduced in the 12th century from North America; Leppäkoski, 1984), the zebra mussel *Dreissena polymorpha* (first observations in 1824), the North American barnacle *Balanus improvisus* (in 1844) and, more recently, the Ponto-Caspian mysid *Hemimysis anomala* (in 1992; Salemaa & Hietalahti, 1993) and the cladocerans *Cercopagis pengoi* (in 1992; Ojaveer & Lumberg, 1995; Gorokhova et al., 2000). However, probably the most successful recent invader in the Baltic Sea is the spionid polychaete *Marenzelleria viridis*. Originally inhabiting North American east coast estuaries, *Marenzelleria* has been found in the North Sea (Essink & Kleef, 1988, 1993; McLusky et al., 1993) and the southern Baltic estuaries since 1985 (Bick & Burckhardt, 1989; Bochert & Bick, 1995). The succeeding years witnessed its rapid spread all over the Baltic Sea (Norkko et al., 1993; Kotta & Kotta, 1998) including the eastern Gulf of Finland and the Gulf of Bothnia (Stigzelius et al., 1997).

After introduction all newcomers must first colonize their immediate surroundings, then adapt to the environment, reproduce, and establish a population in the new habitat (Leppäkoski et al., 1999). The success of the species however depends on its ability to spread from the site of its primary introduction. Common to many successful invaders is a planktonic stage in their life cycle, which allows the population to spread efficiently. As for *Marenzelleria*, the long larval development (4 to 12 weeks) also makes the species prone to transportation within the ballast water of ships (Bochert & Bick, 1995).

After its introduction to Europe, the species was first identified as *Marenzelleria viridis* (Verrill, 1873). However, differences in the spawning time of *Marenzelleria* in the North Sea and the Baltic Sea gave rise to the immigrant's identification problems. In the North Sea, *Marenzelleria* was shown to reproduce in spring (Essink & Kleef, 1993), while in the southern Baltic breeding was only observed from September to November (e.g. Bochert, 1997). Based on genetic analysis, two sibling species were separated in *Marenzelleria viridis*: Type I, inhabiting the North Sea, and Type II, inhabiting the Elbe River estuary and the Baltic Sea (Bastrop et al., 1995, 1997; Röhner et al., 1996; Jürss et al., 1999). Bick & Zettler (1997) also concluded that the morphological features of the adults allow a differentiation of the sibling species as *Marenzelleria* cf. *wireni* (Type I) and *M.* cf. *viridis* (Type II).

In the Gulf of Riga *Marenzelleria* was for the first time found in 1988 near the Daugava River estuary (Lagzdins & Pallo, 1994). The abundance and occurrence of adults has since increased in this area (Lagzdins & Pallo, 1994; Cederwall & Jermakovs, 1999; Cederwall et al., 1999). Notably, in Pärnu Bay, *Marenzelleria* larvae have been found both in spring and autumn.

The abundance of pelagic larvae of *Marezzelleria* is a good indicator of the distribution and development of the species in new habitats. The present paper gives data on the occurrence of *Marezzelleria* larvae in the plankton of Pärnu Bay, NE Gulf of Riga, in 1991–99. The objective is to analyse the life cycle of *Marezzelleria* from the viewpoint of the pelagic stages and to clarify questions regarding their taxonomy and reproduction in the area.

MATERIAL AND METHODS

Study area

Pärnu Bay is a shallow area in the NE part of the Gulf of Riga. The bay can be divided into inner and outer parts, separated by the Liu–Tahku line (Fig. 1). The

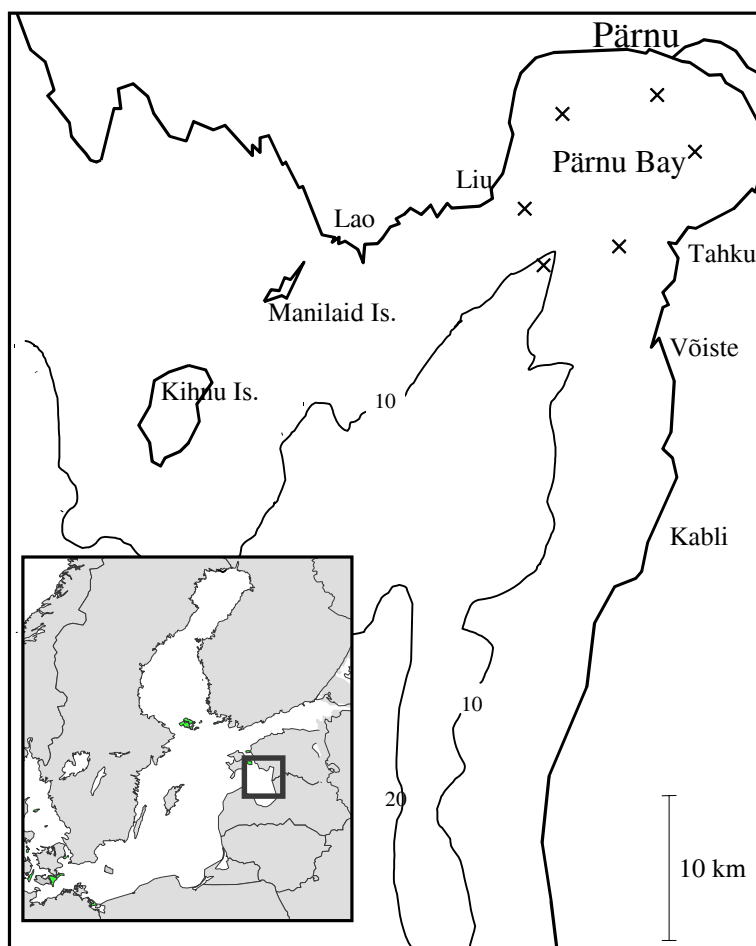


Fig. 1. The study area with the sampling sites.

maximum water depth in the inner part is 7.5 m (average 3.5 m) and in the outer part, 23 m. The volume of the bay (NE of the Manilaid–Kabli line) is 0.7 km³. A total of 1.75 km³ of fresh water is annually supplied by the Pärnu River. Currents are generally weak (0.06–0.07 m s⁻¹), and they depend on the wind direction and speed. After the ice melts, the water temperature rises quickly, exceeding 10°C at the end of May. In July and August the temperature of surface water is over 20°C, and usually remains above 10°C until mid-October. Salinity in the bay varies usually between 4 and 5.5 PSU, except during the spring flood in April, when it declines to 2–3 PSU. The water transparency, visually determined by Secchi disc, is low (usually from 0.8 to 2 m); the visibility depends on the water depth and wind speed, with strong winds resuspending sediment especially in the shallower areas.

Sampling and analysis

Mesozooplankton of Pärnu Bay has been collected since the 1950s with a Juday plankton net (Ø 38 cm, mesh size 90 µm) with vertical hauls from the bottom to the surface. The samples have been preserved in 4% formalin solution and analysed under a binocular microscope. The present paper is based on data obtained during the 1990s, when samples were collected weekly (from the beginning of April to the end of November) at six stations (Fig. 1). All mesozooplankton taxa have been identified, but in this paper only results on *Marenzelleria* and total zooplankton abundances are presented. In the analysis the data were combined to show the average abundances of zooplankton in the inner and outer parts of the bay.

In the zooplankton samples the meroplankton – pelagic larvae of *Bivalvia*, *Cirripedia*, *Gastropoda*, and *Polychaeta* – were also counted. Before the 1990s polychaete larvae (probably *Hediste diversicolor* and *Pygospio elegans*) were only occasionally found in July–August. Since 1991 larvae of *Marenzelleria* have been present in spring and autumn. Since 1999 the younger (fertilized eggs, pre-trochophore, trochophore) and older (setiger) stages of *Marenzelleria* larvae have been counted separately.

At the stations water temperature was measured in the surface and bottom layers. The runoff data for the Pärnu River were obtained from the Estonian Hydro-meteorological Institute.

Statistical analysis

Correlation analysis was used to study the relationship between water temperature (average for measurements at 1 and 10 m depths) and the abundance of *Marenzelleria* larvae in 1992–99. The introduction year 1991 was left out of the analysis. The abundance data for the larvae in the inner and outer parts of

the bay were first $\log_{10}(x + 1)$ -transformed, then both time series were seasonally decomposed to remove the seasonal signal, and Pearson correlations were calculated between these transformed time series. Three periods were analysed separately: (1) the whole period ($n = 248$, April–December each year), (2) spring (from April to June; $n = 64$), and (3) autumn (from September to November; $n = 72$). The time series transformations and correlation analysis were made with Systat 5.03 statistical package.

An identical analysis was performed with *Marezzelleria* larval abundance and runoff data for the Pärnu River. The amount of river runoff serves here as a proxy for water salinity as salinity data were not available for Pärnu Bay.

RESULTS

Occurrence of *Marezzelleria* larvae in Pärnu Bay

In the zooplankton of Pärnu Bay pelagic larvae of *Marezzelleria* first occurred in the outer part of the bay in spring 1991 (Fig. 2). The abundance of larvae was relatively low (ca. 600 ind. m^{-3} ; Table 1). Since then, *Marezzelleria* larvae have been annually present in Pärnu Bay.

In the 1990s *Marezzelleria* larvae did not show any clear abundance trend in the two study areas (Fig. 2). However, in the latest study years the abundance has been high. In the inner part of the bay the average abundance was the highest in 1998 (11 600 ind. m^{-3} in spring and 38 900 ind. m^{-3} in autumn), in the outer part in 1999 (21 300 ind. m^{-3} and 26 000 ind. m^{-3} , respectively; Table 1).

Table 1. Mean abundance of *Marezzelleria* larvae (10^3 ind. m^{-3} ; avg \pm SE) in the inner and outer parts of Pärnu Bay in spring and autumn of the 1990s

Year	Spring (April–June)		Autumn (September–November)	
	Inner part	Outer part	Inner part	Outer part
1991	0	0.6 \pm 0.1	0	6.8 \pm 1.6
1992	1.1 \pm 0.4	0.9 \pm 0.3	0.7 \pm 0.1	3.4 \pm 0.7
1993	0.8 \pm 0.2	3.4 \pm 0.9	1.1 \pm 0.3	1.0 \pm 0.3
1994	2.7 \pm 0.4	1.7 \pm 0.4	8.3 \pm 1.8	5.9 \pm 1.7
1995	1.3 \pm 0.5	0.7 \pm 0.1	6.0 \pm 1.3	3.3 \pm 0.9
1996	7.8 \pm 1.3	2.8 \pm 0.6	9.4 \pm 2.9	5.6 \pm 1.9
1997	2.3 \pm 0.6	1.6 \pm 0.4	1.9 \pm 0.5	2.6 \pm 0.9
1998	11.6 \pm 3.7	0.9 \pm 0.4	38.9 \pm 8.5	12.4 \pm 3.3
1999	12.8 \pm 4.0	21.3 \pm 6.4	10.7 \pm 3.8	26.0 \pm 8.4

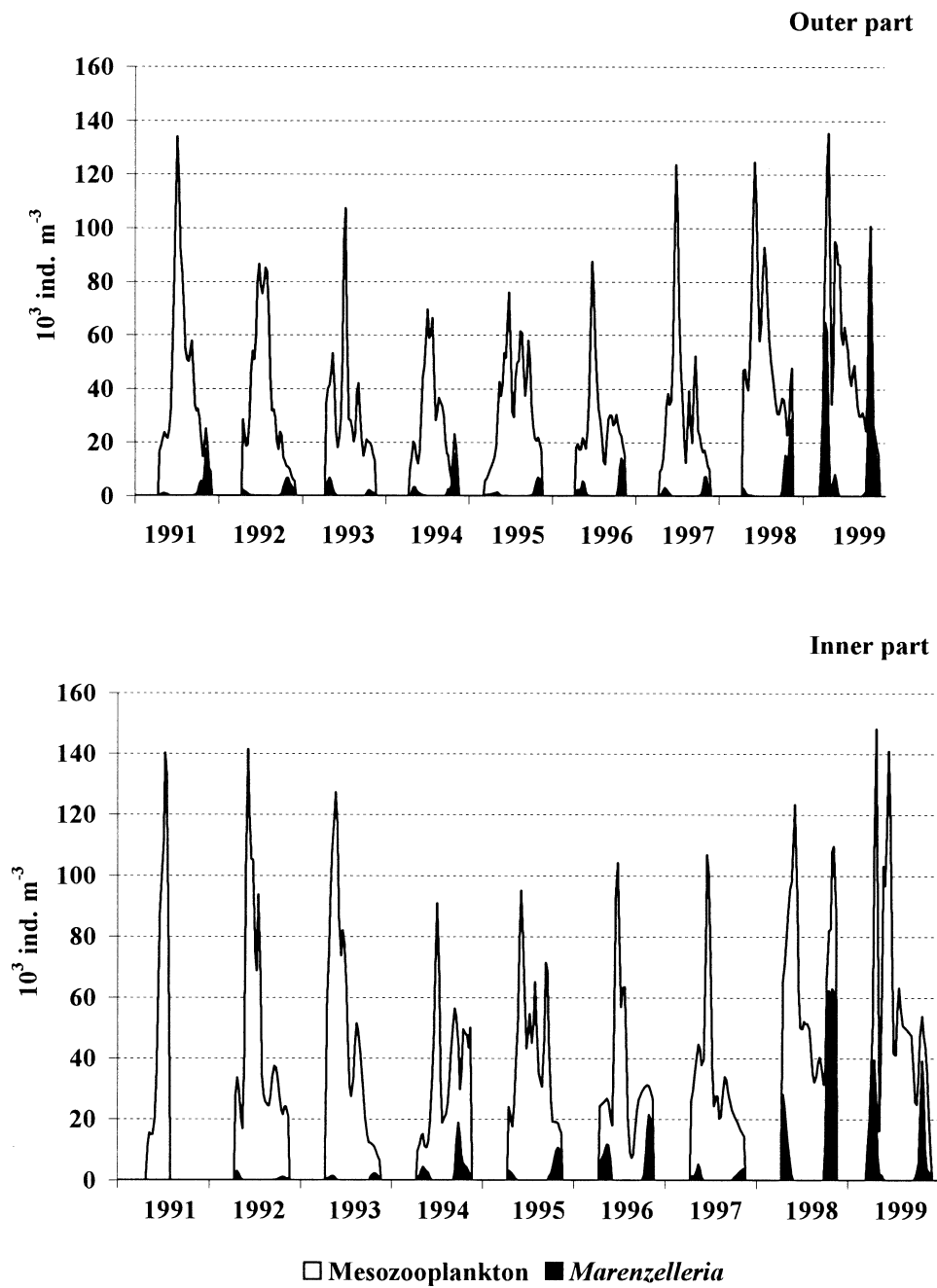


Fig. 2. Abundance of total mesozooplankton and *Marenzelleria* pelagic larvae in different parts of Pärnu Bay in 1991–99.

The relative abundance of larvae in the two parts of the bay has varied irregularly: in some years the abundance has been higher in the inner part, in other years in the outer part of the bay. The dominance has also changed during the same year, with higher abundance in the inner part in spring and lower in autumn, and vice versa.

No statistically significant ($p < 0.05$) correlations were found between water temperature and (log-transformed) larval abundance. The runoff from the Pärnu River showed a weak positive correlation ($0.01 < p < 0.05$) with the larval abundance in the inner part of the bay (Pearson correlation coefficient $r = 0.26$ in spring and 0.24 in autumn) and in the outer part of the bay in spring ($r = 0.28$).

Seasonal succession

Based on data for 1991–99, the larval abundance dynamics in Pärnu Bay can be summarized as follows. Immediately after ice-melt, few *Marezzelleria* larvae occur in plankton, and their abundance usually increases rapidly, peaking in April. The larvae disappear in early June and reappear in late September. Their abundance is the highest in late October or early November. In both parts of the bay the abundance of larvae is usually ca. two times higher in autumn than in spring. During the two peaks the water temperature has been very similar, varying from 4.7 to 7.5°C in spring and from 4.3 to 7.7°C in autumn.

In most years the peaks have occurred almost at the same time in both parts of the bay. Only in 1994 the autumn peak occurred in the inner part in late September and in the outer part of the bay at the beginning of November.

In spring *Marezzelleria* formed on average 58% of the pelagic larvae of the bottom fauna, in autumn their share sometimes exceeded 90%. Of the total mesozooplankton numbers, *Marezzelleria* larvae contributed on average 8–10% in spring and 25–30% in autumn. During their abundance peak, however, they may form 50 to 80% of all mesozooplankton individuals (Fig. 2).

Larval stages in 1999

In March 1999 a few older, setiger stages of *Marezzelleria* were found in the plankton samples. In early April all pelagic stages – fertilized eggs, pre-trochophore, trochophore, and setiger stages – occurred in plankton. Younger pelagic stages were present until the end of April. In the outer part of the bay they were more abundant than the setiger stages. In the inner part of the bay the younger stages peaked 1 to 2 weeks later than in the outer part (Fig. 3).

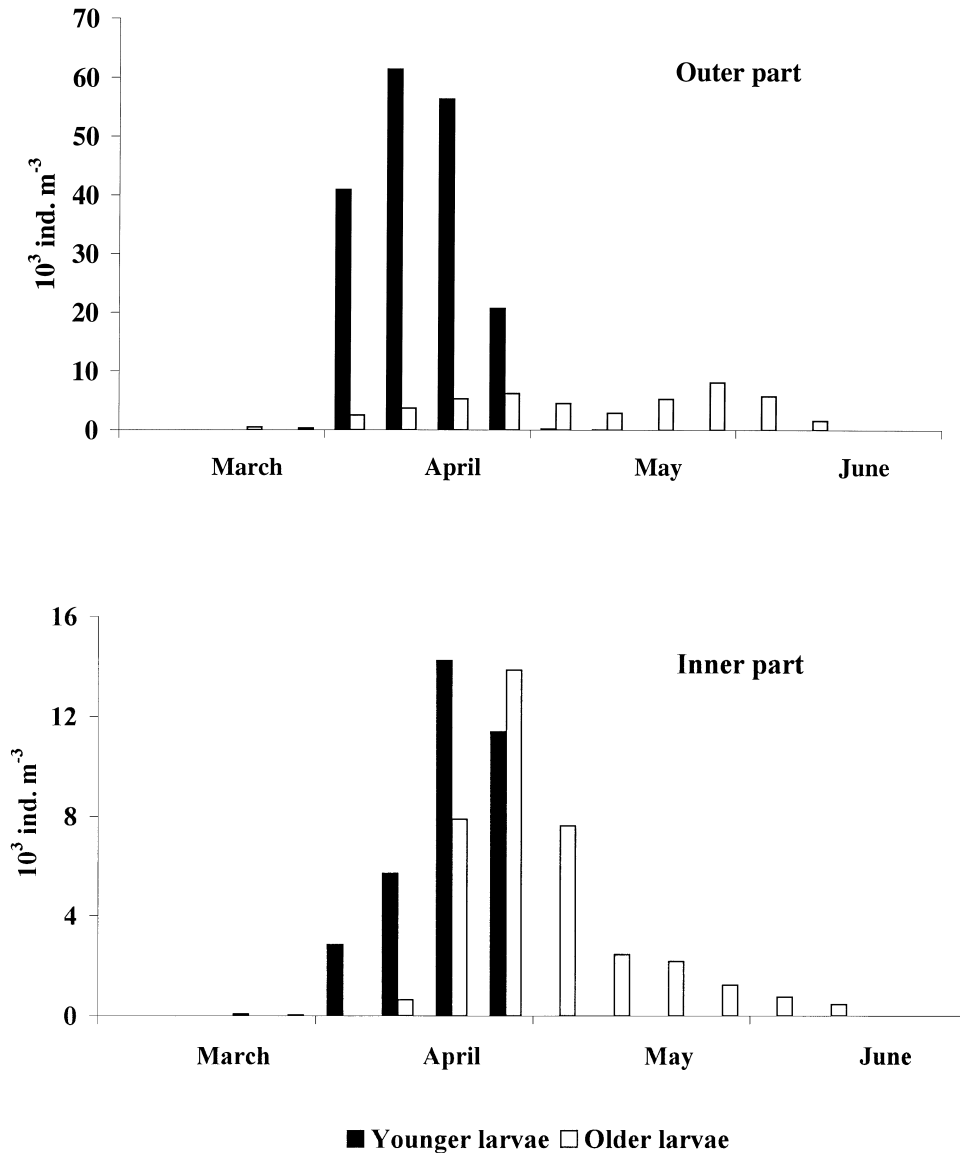


Fig. 3. Abundance of *Marenzelleria* younger (fertilized eggs, trochophores) and older (setiger) larvae in the inner and outer parts of Pärnu Bay in the spring of 1999.

In autumn, starting from October, all pelagic stages, including fertilized eggs, were present in plankton (Fig. 4). The abundances of all stages reached their maxima earlier in the inner part of the bay (in late October) than in the outer part of the bay (in early November).

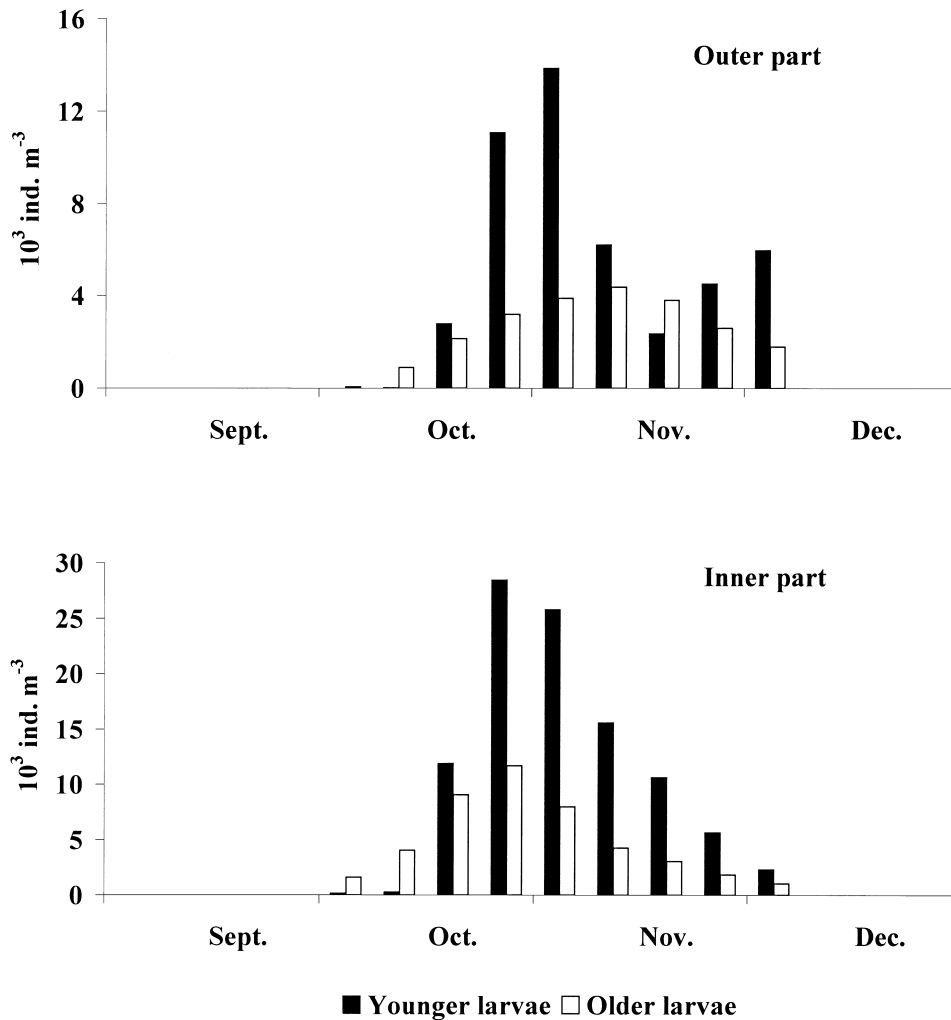


Fig. 4. Abundance of *Marenzelleria* younger (fertilized eggs, trochophores) and older (setiger) larvae in the inner and outer parts of Pärnu Bay in the autumn of 1999.

DISCUSSION

Long-term dynamics

After the first recording of *Marenzelleria* in the southern Gulf of Riga in 1988, its abundance increased during the four succeeding years (Lagzdins & Pallo, 1994). In 1994 and 1995, the maximum abundance of *Marenzelleria* adults in the sediments of the Gulf of Riga exceeded 2000 ind. m⁻², the average being ca. 100 ind. m⁻² (Kotta & Kotta, 1998; Pallo et al., 1998; Cederwall & Jermakovs,

1999; Ojaveer et al., 1999). In Pärnu Bay a relatively low larval abundance during 1991–97 was followed by a strong increase only in 1998–99 (Fig. 2). Such a long interval between the first record and increase in abundance is unusual for the Baltic Sea. A clear increase in the *Marenzelleria* abundance is usually observed 2 to 5 years after introduction (Stigzelius et al., 1997; Zettler, 1997). The relatively high temperature and high productivity of the Gulf of Riga should favour larval development in the area (cf. Burckhardt et al., 1997). The slow population increase in Pärnu Bay is thus surprising.

Marenzelleria cf. *viridis* adults survive in practically fresh water (down to 0.03 PSU) (Fritzsche & von Oertzen, 1995), but the larval stages are much less tolerant to low salinity. The 3-setiger larval stage is especially vulnerable, since the yolk reserves have been exhausted and the larva starts external feeding. At water salinities below 5 PSU the 3-setiger larvae do not develop further, although, at 5°C they may survive for 2–3 weeks (Bochert, 1997). In Pärnu Bay, especially in its inner part, the salinity of water declines below 5 PSU in spring, which may slow down the development of the spring generation. This may also be the reason for the delayed increase in the larval abundance in Pärnu Bay. This hypothesis could however not be confirmed, since salinity data were not available for Pärnu Bay. It is not clear why the correlations between the runoff data and abundance of *Marenzelleria* larvae were weakly positive. However, the fraction of explained variance (r^2) was very low (<8%), which allows no firm conclusions. It must be noted that statistical analysis of abundance data of an introduced species is very difficult: it is not obvious that any clear relationships can be found between environmental data and the abundance of a species expanding its population in a new habitat. Analysis of larval abundance is especially problematic, since the abundance of larvae at a fixed station depends on reproductive success of adults, advection of larvae with currents, and survival of larvae in the ambient environmental conditions.

Seasonal dynamics

Based on the occurrence of fertilized eggs and trochophores in plankton it can be concluded that *Marenzelleria* reproduces in Pärnu Bay both in spring and autumn. In spring spawning starts at ice-melt and continues until late April. In autumn reproduction begins in September and lasts until December. In all likelihood, *Marenzelleria* does not spawn under ice in winter. This bimodal larval abundance pattern differs from that in other parts of the Baltic Sea, where larvae are mainly found only in autumn (e.g. Bochert & Bick, 1995; Kube et al., 1996; Bochert, 1997; Daunys et al., 2000).

Differences in spawning times have triggered detailed studies into the taxonomy of *Marenzelleria viridis* in the North Sea and the Baltic Sea. Bastrop et al. (1997) separated the two groups to different sibling species and proposed that the different spawning seasons are genetically determined. Since in Pärnu Bay *Marenzelleria* larvae also occur in spring and autumn, both Type I and Type II could be present. However, as Type I apparently prefers a higher salinity than

occurs in Pärnu Bay (Röhner et al., 1996), and as genetical studies have shown that only *M. cf. viridis* (Type II) inhabits the Gulf of Riga (Bastrop et al., 1997), we believe that in this bay both larval peaks are produced by the same sibling species – *M. cf. viridis*.

The autumn spawning of *Marenzelleria* in the southern Baltic Sea was first explained by favourable environmental conditions, mainly temperature (Zettler et al., 1995; Bochert et al., 1996). In the southern Baltic water temperature rises rapidly above 20°C in spring, *M. cf. viridis* become sexually mature and reproduce already during their first autumn. In the North Sea estuaries, in contrast, tides cause great variations in water temperature and salinity. Adult *Marenzelleria* probably use much energy for maintenance, and gametes are not yet fully developed in autumn. By the time the individuals are ready for reproduction, water temperature is already too low for successful larval development. Consequently spawning is delayed until the next spring (Bochert et al., 1996).

In the Gulf of Riga, like in the whole Baltic Sea, tides are absent, but the temperature conditions are somewhat harsher than in the southern Baltic. Water temperature usually rises above 20°C only in the middle of July. Nevertheless, in Pärnu Bay the greater part of *Marenzelleria* population reproduce in autumn. Evidently the species produces several, partly overlapping, generations or cohorts per year. In the southern Gulf of Riga three adult generations (Cederwall & Jermakovs, 1999) have been distinguished. How these three generations can produce two larval peaks is not obvious. The growth rate and survival of *Marenzelleria* larvae depend on salinity, temperature, as well as food concentration and quality (Bochert, 1997; Burckhardt et al., 1997). It can be hypothesized that the larvae that are born in early April can utilize the phytoplankton spring bloom and develop rapidly in the warm summer temperatures. Like their conspecifics in the southern Baltic, they mature early and reproduce during their first autumn. In contrast, the larvae that are born later in spring develop slower and their spawning takes place only during the next spring. Detailed life history studies are however needed to establish the reproductive pattern of *Marenzelleria cf. viridis* in Pärnu Bay.

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***Marenzelleria viridis*'e (Polychaeta: Spionidae) pelaagiliste vastsete arvukuse dünaamika Pärnu lahes aastail 1991–1999**

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Põhja-Ameerikast pärinev polüheet *Marenzelleria viridis* määrati esmakordselt Läänemeres 1985. ja Liivi lahes 1988. aastal. Alates 1991. aastast on *Marenzelleria* pelaagilised vastsed esinenud igal aastal Pärnu lahe planktonis. Vastsete suhteliselt püsiv arvukus kasvas hüppeliselt aastail 1998–1999. Läänemere puhul erandlikult pikk ajaline vahe liigi ilmumise ja massilise arengu vahel on ilmselt tingitud vee vähesest soolsusest Pärnu lahes. Lääne- ja Põhjamerel on määratud kaks erinevat *Marenzelleria* vormi, paarisliiki. Põhjamerel esinev vorm, *M. cf. wireni*, paljuneb kevadel, Läänemere vorm, *M. cf. viridis*, aga sügisel. Pärnu lahes esinevad *Marenzelleria* viljastatud munad ja trohhofoorvastset nii kevadel kui ka sügisel. Seega kerkib kevadiste vastsete liigilise kuuluvuse küsimus. Kuna geneetiliste uuringute alusel esineb Liivi lahes vaid *M. cf. viridis*, võib oletada, et sobivates keskkonnatingimustes paljuneb see liik kaks korda aastas. *M. cf. viridis*'e paljunemise aeg ei ole määratud mitte geneetiliselt, vaid see sõltub väliskeskkonna oludest, tõenäoliselt peamiselt vee temperatuurist ja toitumistingimustest.