

VARIATION IN THE REPRODUCTIVE STATUS, LARVAL OCCURRENCE AND RECRUITMENT IN AN ESTUARINE POPULATION OF *MARENZELLERIA VIRIDIS* (POLYCHAETA: SPIONIDAE)

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ABSTRACT

Since its immigration in 1985, the spionid polychaete *Marenzelleria viridis* (Verrill, 1873) has become a major element of the fauna in the Darss-Zingst Bodden Chain, a tideless estuary-like coastal water of the southern Baltic. High abundances of the pelagic larvae were found in this area in autumn.

The reproduction of *M. viridis* was investigated from March 1992 to April 1995 at an inner station (salinity 2-6‰) and an outer station (salinity 4-12‰) of the estuary. Adult animals were collected once a month and the reproductive stage was ascertained. Plankton samples were taken twice a week during the spawning season, and the pelagic larvae were counted. The recruitment of juvenile worms was observed by benthos samples. Gametogenesis began in May, and the animals reached maturity at the end of September in 1992, but gametogenesis lasted one month longer in 1993 and 1994. Maximum larval densities were highest in 1992 (about $22 \cdot 10^6$ ind./m³), reached $1 \cdot 10^6$ ind./m³ in 1993 and 314,000 ind./m³ in 1994. In 1994 the salinity was unusually low and few larvae reached metamorphosis (16 to 17-setiger stage) in 1994. Recruitment started in mid-October and juveniles were most abundant in 1993. Also spatial differences in the proportion of spawning animals and larval density were observed.

The way of successful colonization of the oligohaline regions of the estuary is discussed.

INTRODUCTION

The Darss-Zingst Bodden Chain (DZBC) is a tideless estuary-like coastal water of the southern Baltic. It is characterized by decreasing salinity from east (about 10-12‰) to west (nearly fresh water). The DZBC was colonized by a few polychaete species until 1985, namely the sabellids *Fabricia sabella*, *Manayunkia aestuarina*, the ampharetid *Alkmaria romijni*, the spionids *Polydora ciliata*, *Pygospio elegans*, *Streblospio shrubsoli*, and the nereids *Nereis diversicolor* and *Neanthes succinea*. The distribution of these species was limited to the outer regions of the DZBC where the salinity does not drop below 5‰. At that time, the macrozoobenthos of the oligohaline part of the DZBC was dominated by

chironomids and oligochaetes, which accounted for up to 75 to 95% of all individuals (Arndt 1988, Zettler 1994).

Since the late eighties, an invader, the euryhaline species *Marenzelleria viridis*, a typical representative of estuarine communities, has become established in these waters (Bick & Burckhardt 1989). The species has penetrated into the oligohaline regions in such large numbers that it has displaced the chironomids and oligochaetes from their position as the most common macrozoobenthos representatives in this zone. In 1993, *M. viridis* achieved abundances of 8,000 ind./m² in the oligohaline areas (Zettler 1994). The worms inhabit vertical, mucus-lined burrows up to 35 cm deep both in sandy (Hines & Comtois 1985, Essink & Kleef 1993, Zettler et al. 1994) and muddy sediments (Gruszka 1991).

Gametal and larval development of this spionid worm was investigated by George (1966 syn.: *Scolecopelides viridis*), Bochert & Bick (1995a, b) and Bochert (1996a, b). Larval development is entirely pelagic and the fertilized egg is the first planktonic stage. The metamorphosis into benthic juvenile stages takes place at the 16 to 17-setiger stage after a pelagic phase of 5-6 weeks at 10°C or 10 weeks at 5°C (Bochert & Bick 1995b, Bochert et al. 1996).

In Northamerican estuaries (Nova Scotia) gametogenesis takes place from October to March (George 1966). Pelagic larvae and juvenile benthic *M. viridis* are found in spring (George 1966, Simon 1968, Boesch et al. 1976, Whitlatch 1977, Holland et al. 1980, Jordan & Sutton 1984). The worms also reproduce in spring in North Sea estuaries (Atkins et al. 1987, Essink & Kleef 1988, 1993). Dauer et al. (1980, 1982) found sexually mature *M. viridis* in nocturnal plankton holes during ebb tides in February and juvenile animals two weeks later during flood tides in Lafayette River (Virginia). The authors speculated that the worms disperse down the estuary, where the salinity is in the lower mesohaline to oligohaline range, to more physiologically favorable regions for spawning and that juveniles disperse up the estuary to colonize the oligohaline regions, where they attain their highest abundances (Boesch et al. 1976, Dauer et al. 1982).

The purpose of the present study was to analyze the reproductive strategy of *M. viridis* in a brackish water estuary of the southern Baltic and to clarify the way of successful colonization of the oligohaline regions of the investigated area.

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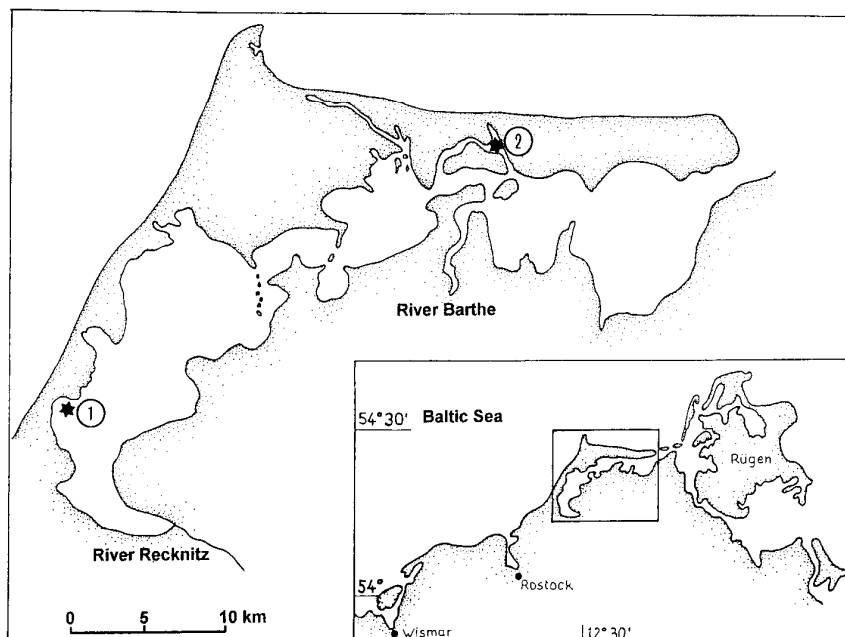


Fig. 1. Map of the Darss-Zingst Bodden Chain showing the location of the stations.

MATERIAL AND METHODS

The DZBC is a tideless estuary on the south coast of the Baltic. It consists of four consecutive boddens linked by narrow straits (Fig. 1). Salt-rich water (10–12‰) enters the DZBC from the east through the narrow mouth. Freshwater is supplied to the boddens mainly by the Rivers Recknitz and Barthe. The salinity ranges from nearly freshwater in the western part to 12‰ in the east. The boddens are very shallow, the mean water depth varying between 1.5 and 2.0 m (max.: 4.0 m).

Two sites were chosen for the investigation: one in the inner part, station 1, and one in the outer part, station 2 (Fig. 1). Gametogenesis was studied by collecting animals once a month from these two nearshore stations for three years. About 20–30 animals were collected by means of a corer (78.5 cm² sample area, 40 cm deep) on each sampling day. The worms were held in 500 ml plastic vessels filled with biotope water for two days to empty their guts. They were then anaesthetized in sea water (10‰) containing 20% MgCl₂ for 30 minutes and subsequently fixed in Bouin's solution or 4% Baker's formaldehyde. The mid-part of the animals were embedded in paraffin wax or glycol-methacrylat, sections (3–5 μm) were produced and stained with hemalun/eosine. The stage of gamete maturity was ascertained.

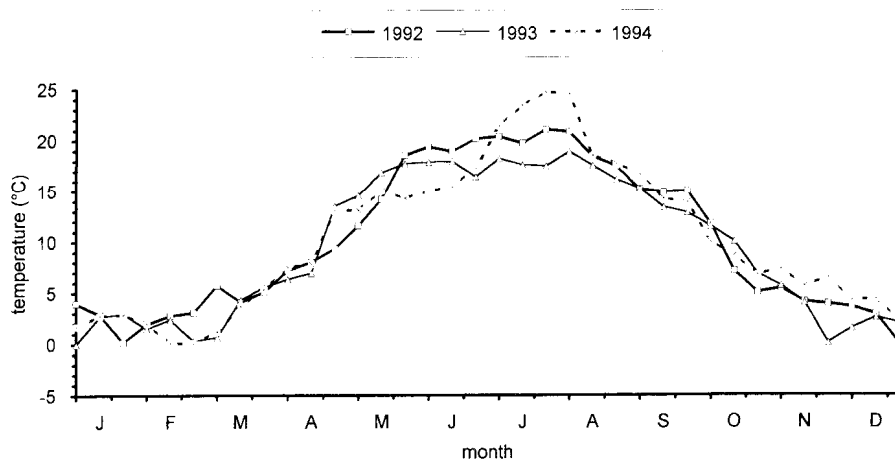


Fig. 2. Water temperatures (mean values from daily observations) at station 2 in 1992 to 1994.

Larval development was studied by collecting plankton samples (300 ml to 100 l) once a month outside of the reproductive period and twice a week during it. Three parallel samples (in 1993 and 1994 only one sample) were filtered through a 120 μm net on each sampling day, and the numbers of *M. viridis* larvae were counted and sorted according to the number of segments.

Meiobenthos samples were taken with a corer (19.6 cm² sample area, 5 cm deep) from October to March of each reproductive season to study the recruitment of juvenile *M. viridis*. Three corer samples were taken on each sampling day, washed over a 300 μm sieve and fixed in 4% formaldehyde. The samples were analyzed under a dissecting microscope (Olympus BH-2, Germany) in the laboratory.

Salinity and water temperature were measured by daily observations at a field station/laboratory (st. 2). Additional measurements were made at st. 1 on each sampling day by means of an LF 95 (WTW, Germany) conductance measuring unit.

RESULTS

Abiotic conditions

Water temperatures in the DZBC showed a cyclical trend, even though the monthly means for May to August were 2-3°C lower in 1993 than in 1992 (Fig. 2). In 1994 the water temperatures were generally below 17°C until late June and remained substantially higher than in the two previous years throughout July.

Annual and interannual salinity variations in the investigated area were considerable. At st. 1, the mean salinity exceeded 5‰ only from September 1992 to August 1993, varying between 4.5 and 6.5‰ during this period (Fig. 3a). It

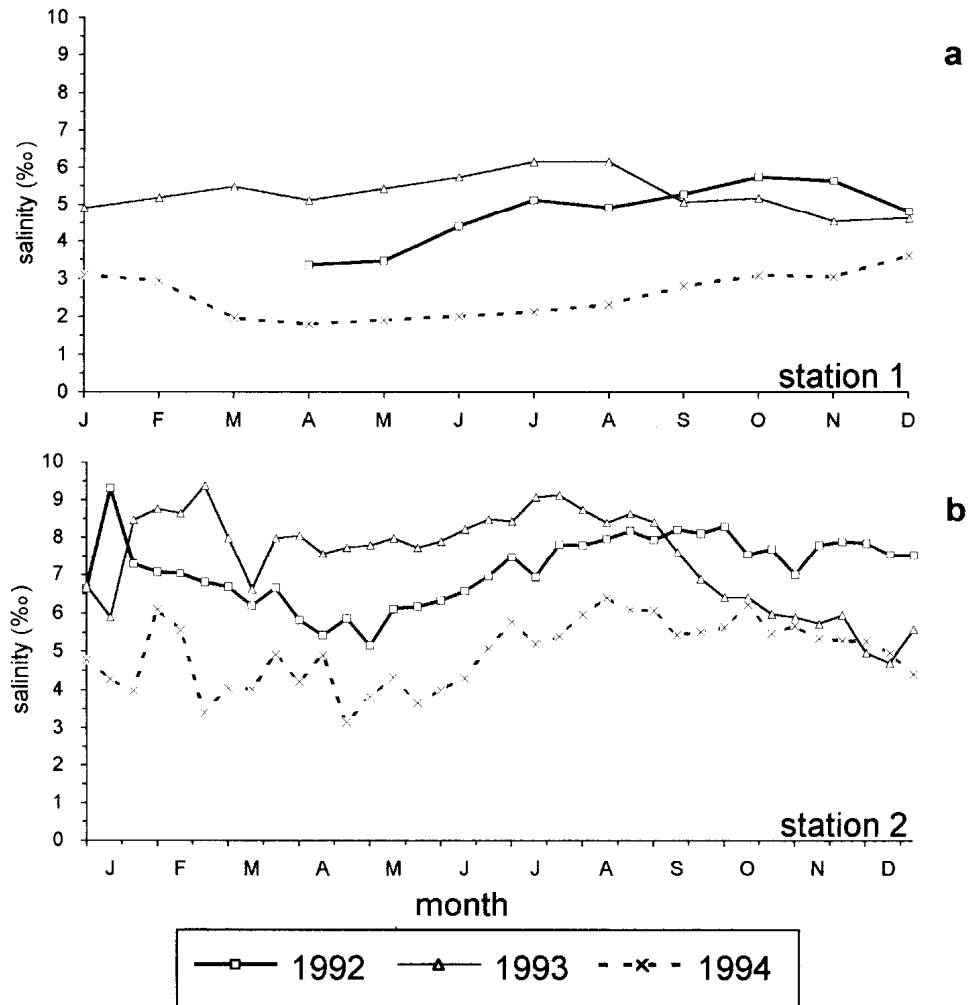


Fig. 3. Salinity in 1992 to 1994, a) station 1 and b) station 2.

decreased drastically in early 1994, and fluctuated between 2 and 4‰ thereafter.

At st. 2, salinity was above 5‰ throughout 1992, increased in August 1992 and remained about 8‰ until August 1993. In late November 1993 salinity dropped to about 5‰ (Fig. 3b). In 1994, the salinity at st. 2 varied between 3 and 6‰.

Gametogenesis and spawning

Gamete formation started between mid-May and mid-June in all three years of the study. In 1992, gametes were found in over 60% of the animals at the end of June (Figs. 4a, 5a), but in 1993 and 1994 this proportion was not reached

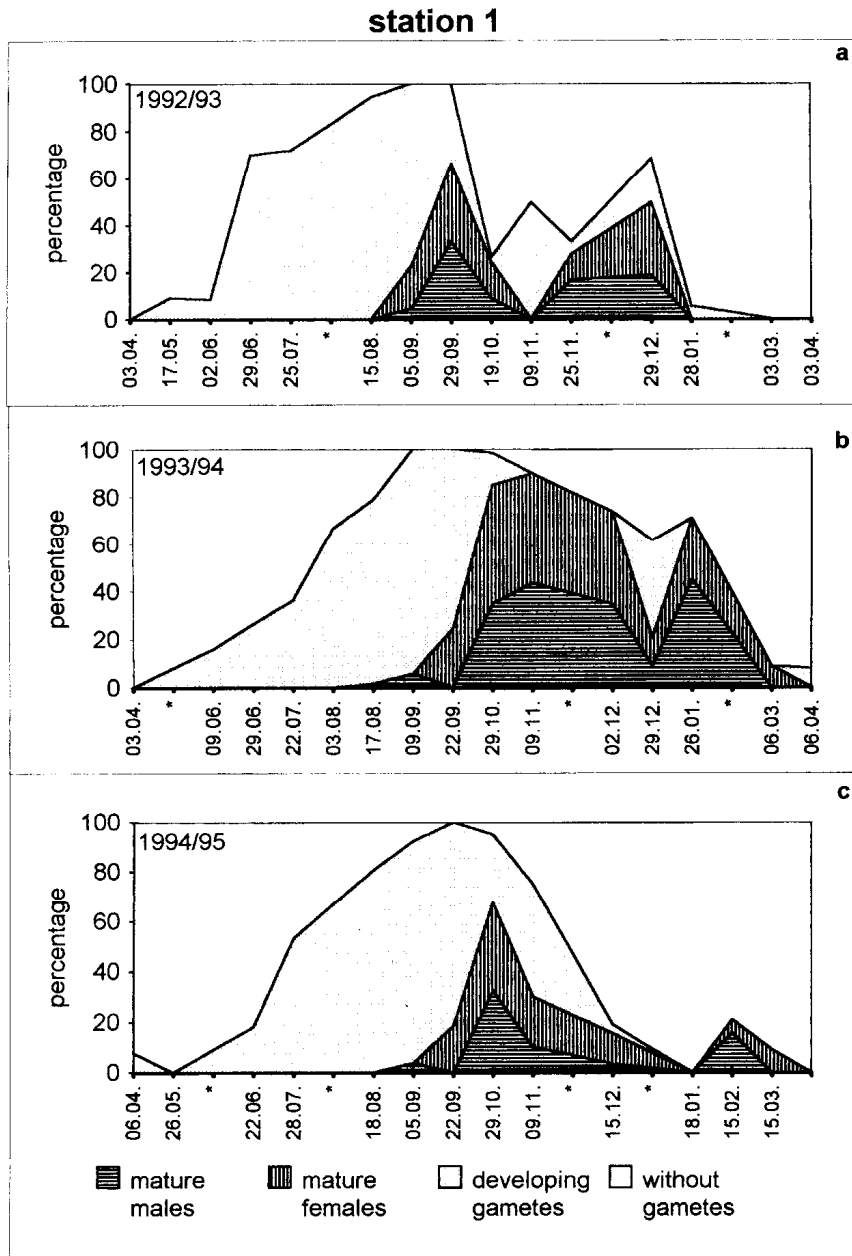


Fig. 4. Gamete stages (percentage of animals) of *Marenzelleria viridis* at station 1 in 1992 to 1995.

until late July (Figs. 4b, c, 5b, c). Gamete development continued for 4-5 months, the population starting to spawn in late September in 1992 and late October in 1993 and 1994. Gametogenesis was roughly synchronous in males and females (Figs. 4, 5).

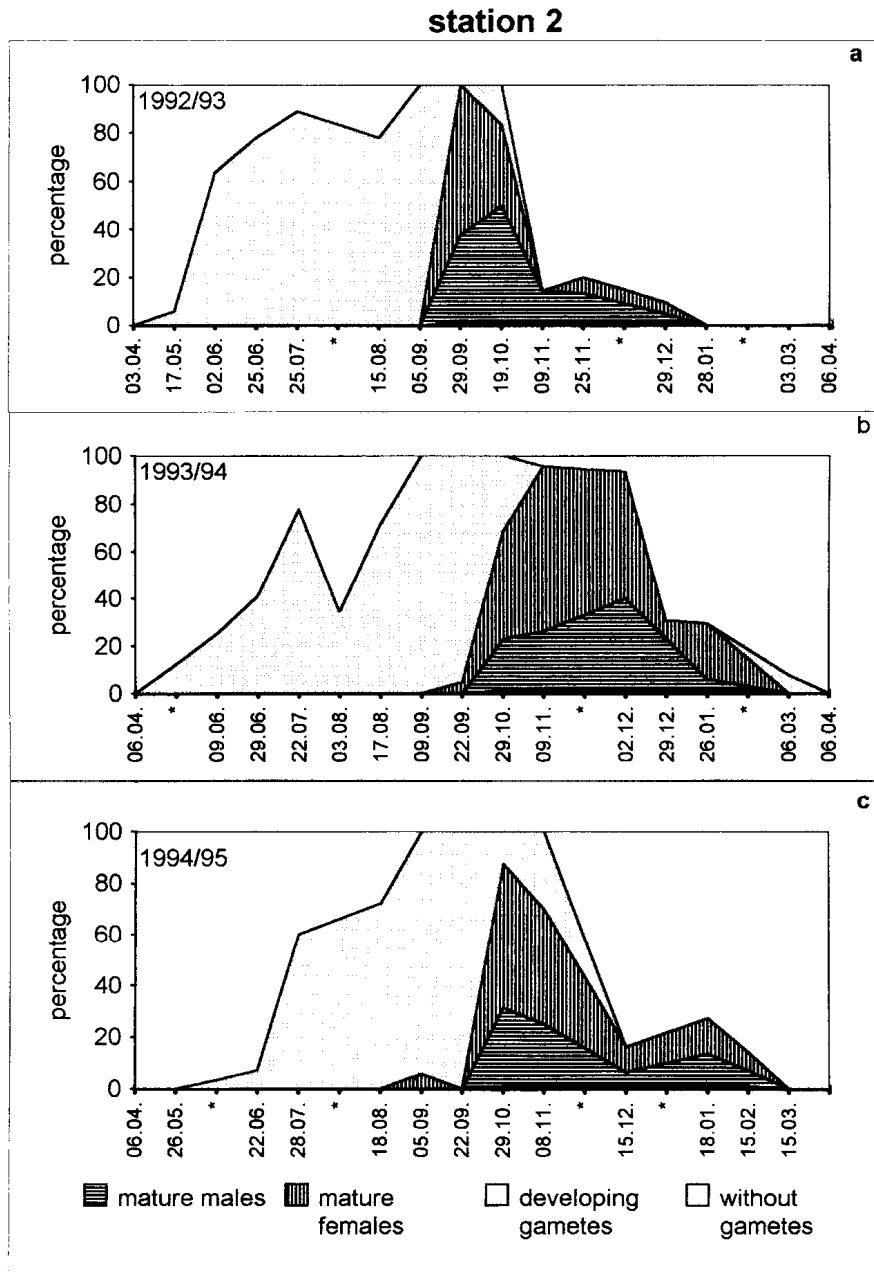


Fig. 5. Gamete stages (percentage of animals) of *Marenzelleria viridis* at station 2 in 1992 to 1995.

In 1992, almost all ripe animals had spawned by early November and 20-50% of the animals were ready to spawn again after a second short period of gametogenesis (Figs. 4a, 5a). Animals with ripe gametes were not found in late January 1993.

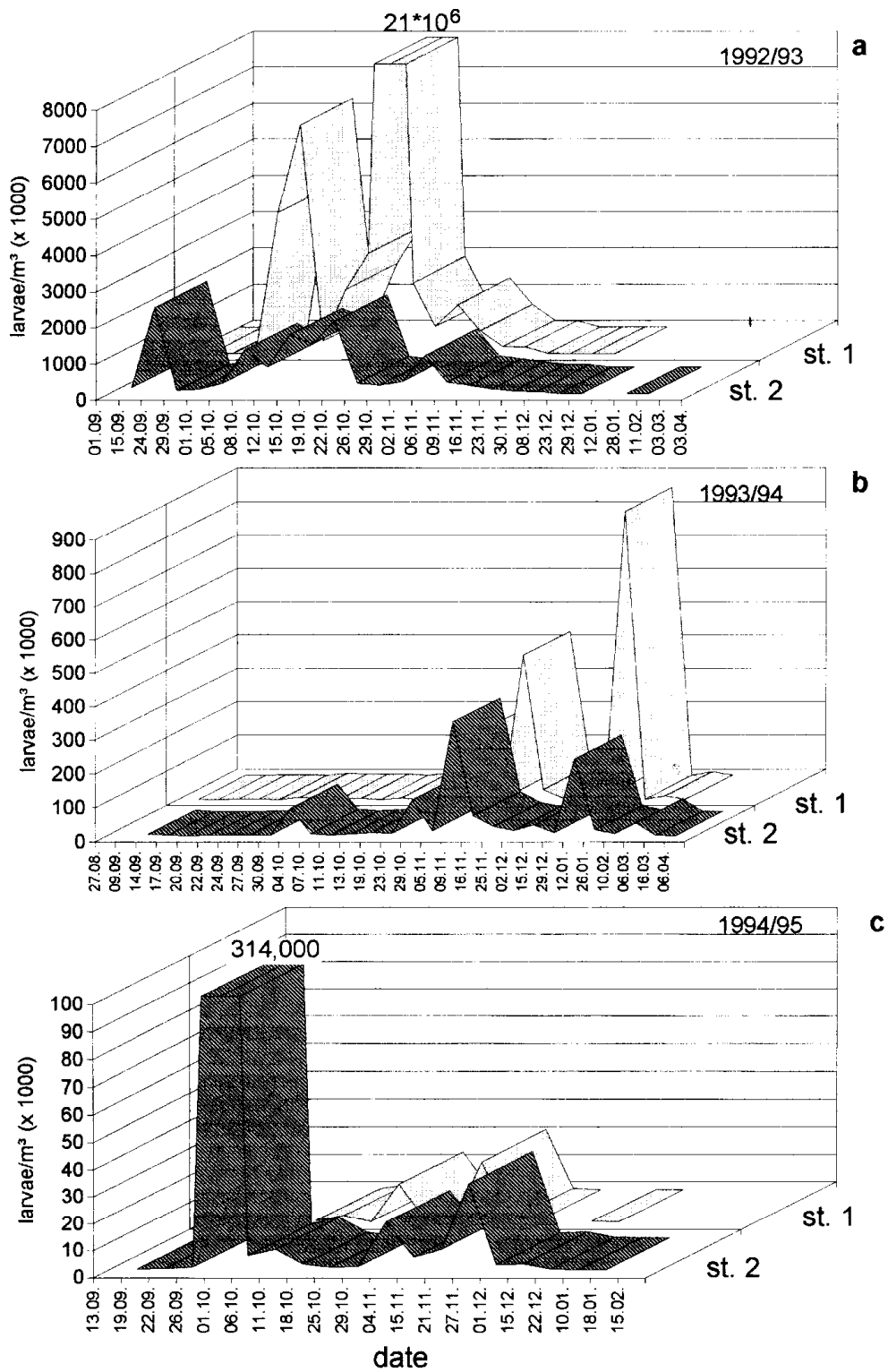


Fig. 6. Occurrence and abundances of *Marenzelleria viridis* larvae at two stations in a) 1992/93, b) 1993/94 and c) 1994/95 reproductive season.

In 1993, a large proportion of the population bore ripe gametes at the end of October, but there was no outburst of spawning: 74-93% of the animals still carried ripe gametes in early December, and 30-71% even in late January 1994 (Fig. 4b, 5b). This pattern was repeated in the 1994 spawning season, when the first animals were ready to spawn in late October (Figs. 4c, 5c). However, the proportion of animals that had reached this stage by mid-November was much smaller than during the 1993 season. Ripe gametes were still found in 21-28% of the animals examined up to mid-February 1995 (Figs. 4c, 5c).

No major differences in time were observed between the course of gametogenesis at the two stations, gamete formation and the release of ripe gametes respectively starting at about the same time at both. However, the stations did differ in the proportion of spawning animals. Between 87 and 100% of the animals achieved sexual maturity at st. 2, whereas it was 66-90% at st. 1 (Figs. 4, 5). The production of a second batch of gametes after the first spawning was observed at both stations, the proportion of animals producing a second batch of ripe gametes varying between 20% and 71%.

Occurrence of pelagic larvae

Larvae appeared in the plankton in low abundances from early September onwards in all years of the investigation (Fig. 6).

Spawning was particularly intensive in late September during the 1992 season. At st. 2, early stages (eggs and 1-setiger larvae) were found until January 1993, but were most abundant in September and October when the spawning population was most abundant. Only few dead eggs were found. Larval abundances exceeded $1 \cdot 10^6$ ind./m³ in late September and then increased rapidly, peaking at over $21 \cdot 10^6$ ind./m³ in mid-October (Fig. 6a). The successful development of the larvae in 1992 is documented by the appearance of 10-setiger stages in abundances exceeding 100,000 ind./m³ in early October. These animals were well on the way towards the 16 to 17-setiger stage at which they assume the benthic life of juveniles (Figs. 7a, 8a). Total larval abundances then decreased to less than 1,000 ind./m³ by mid-December, and the last larvae from this season were found in the plankton in mid-February 1993 (Fig. 6a).

In contrast, early planktonic stages from the 1993 spawning season were still found in the plankton up to April 1994. Huge numbers of dead eggs were found among the plankton during the whole of the 1993 reproductive season. Total larval densities were much lower during the 1993 season than in 1992, not reaching values of around 400,000 ind./m³ until early November (Fig. 6b). In contrast to the 1992, when less than 1,000 larvae/m³ were found in the plankton from mid-December onwards, larval densities in 1993 reached their maximum of almost $1 \cdot 10^6$ /m³ in late December. They then remained high (10,000 to 40,000 ind./m³) until early March 1994 (Fig. 6b). As in the previous season, larvae with more than 10 setigers were found among the plankton

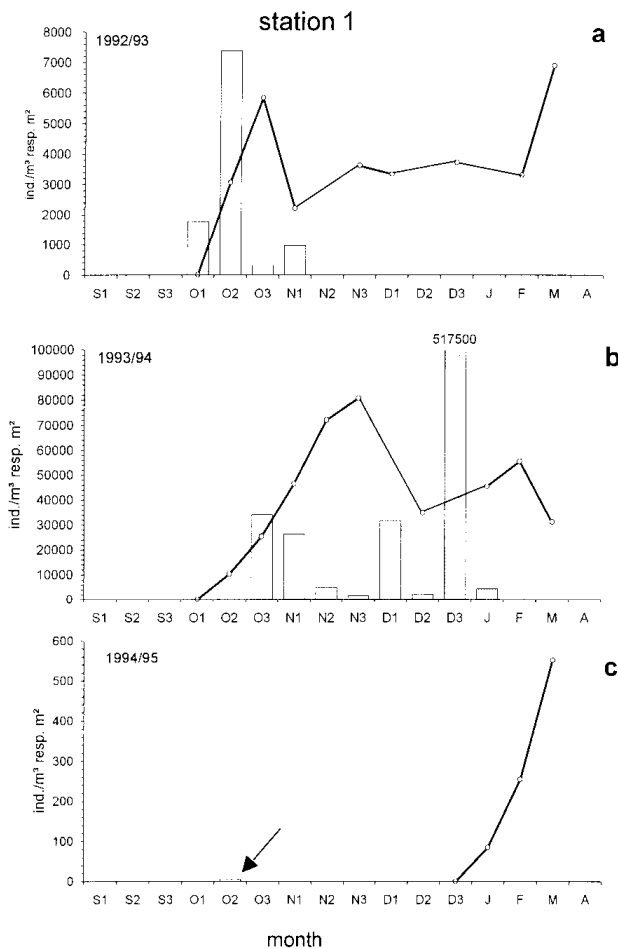


Fig. 7. Mean abundances of *Marenzelleria viridis* larvae >10 setigers (ind./m³) (bars) and abundances of juvenile benthic animals (ind./m²) (lines) at station 1 from September to April in three reproductive seasons. Numbers in x-axis denote 1st to 3rd decades from September to December.

from early October onwards in 1993, and their abundance started to increase appreciably at the end of October (Figs. 7b, 8b). Larvae of this size were still present among the plankton in early March 1994.

The pattern in 1994 closely resembled that in 1993, early larval stages first appearing in mid-September and being found in the plankton only until mid-December. Early larval stages and dead eggs were found in approximately equal numbers. Total larval abundances were lower than in the 1993 season, the maximum of 314,000 ind./m³ being reached in early October (Fig. 6c). As in 1992, larval densities dropped below 1,000 ind./m³ by mid-December, but larvae had vanished from the plankton by the end of January 1995. A few larvae (about 1000 ind./m³) with more than 10 setigers were found in early October 1994 and densities of these increased up to 13,000 ind./m³ in mid-November (Figs. 7c, 8c).

The two stations differed clearly during the 1992 and 1994 reproductive seasons in terms of both larval density and its variation in time. Larval densities

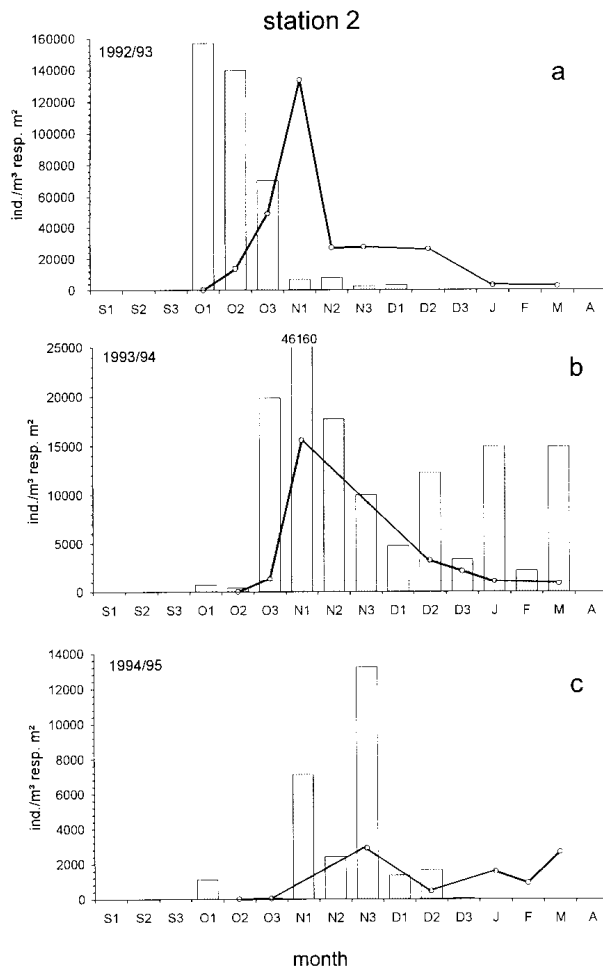


Fig. 8. Mean abundances of *Marenzelleria viridis* larvae >10 setigers (ind./m³) (bars) and abundances of juvenile benthic animals (ind./m²) (lines) at station 2 from September to April in three reproductive seasons. Numbers in x-axis denote 1st to 3rd decades in September to December.

decreased more rapidly at st. 1 than at st. 2, dropping to below 1,000 ind./m³ by mid-November at st. 1, but not until four weeks later at st. 2. Differences were also observed in the numbers of larvae with more than 10 setigers, the larval community at st. 1 consisting mainly of individuals with less than 10 segments in 1992 and almost exclusively of such larvae in 1994 (Fig. 7a, c).

Recruitment

The first juvenile animals were found in mid-October, whereafter their abundance increased rapidly to peak between the end of October and the end of November in 1992 and 1993 (Figs. 7, 8).

At st. 1, juvenile abundance had reached almost 6,000 ind./m² by mid-October in 1992, declined by about 50% by February 1993 and then increased again to almost 7,000 ind./m² (Fig. 7a), whereas at st. 2 the juvenile abundances were much higher, ranged from 13,000 to 134,000 ind./m² in late fall and decreased to 2,500 ind./m² in mid-March 1993 (Fig. 8a).

The tables turned in 1993 when juveniles were more abundant at st. 1. Their abundance decreased from 80,000 ind./m² in late November (15,000 ind./m² at st. 2) to slightly more than 30,000 ind./m² in March 1994 (850 ind./m² at st. 2) (Figs. 7b, 8b).

The values recorded for the 1994 season were even lower than in 1992 and 1993, only 42 ind./m² having colonized the sediment by the end of October at st. 2. A month later, the figure had risen to almost 3,000 ind./m² and about the same value was recorded in March 1995 (Fig. 8c). The first juveniles at st. 1 were found in late January 1995 at an abundance of 85 ind./m². Their abundance had increased to 552 ind./m² by March 1995 (Fig. 7c).

DISCUSSION

Marenzelleria viridis is a discrete polycyclic species with a well defined breeding season (autumn in the southern Baltic). Gametal development takes 4-5 months, during which the water temperature is above 10°C. During gametal development, the *M. viridis* population in the DZBC is exposed to various factors such as salinity and temperature fluctuations, oxygen deficiency, hydrogen sulphide, variations in food quality and quantity, the compound effects of which influence the duration and success of gametal development. Besides consuming energy (resources) for adaptation to variations in environmental parameters, i.e. metabolic performance, and juvenile growth, the animals must invest additional resources during gametal development to ensure future reproductive output (Olive 1992).

In the studied population, gametal development started between mid-May and mid-June. Seasonal and spatial variations were slight and may even result from the difficulty of localizing the gonads at this early stage.

Greater variation was observed in the time of readiness for spawning. Most of the population reached this point a month later in 1993 and 1994 than in 1992. Over 87% of the individuals at st. 2 achieved ripeness in all three years, whereas only 66-68% of the animals at st. 1 reached this stage in 1992 and 1994. The delay in spawning or inability to spawn may have been caused by food deficiency or increased energy consumption for metabolic processes due to environmental stress conditions.

As far as nutrition concerned *M. viridis* is a surface deposit and suspension feeder (Dauer et al. 1981) and generally finds sufficient food in the eutrophic to hypertrophic DZBC (Schiewer et al. 1994), where the mean organic content of the top 5 cm of the sediment varies between 1.4 and 9.1% DW (Schlungbaum et al. 1994).

By contrast environmental stress could be more important. The effect of salinity on gametogenesis is known for several polychaete species (Schroeder & Hermans 1975). *M. viridis* has the ability to survive in brackish waters with salinities down to 0.01‰ (Bochert et al. 1996). The animals must hyperregu-

late the osmolarity in their bodies at salinities below 5‰ (Fritzsche 1995). Their metabolic activity is therefore higher under oligohaline conditions, and this stress situation is reflected in reduced survival times determined in laboratory experiments (Fritzsche & von Oertzen 1995a). The salinity was higher than 5‰ at both stations in 1992 and 1993, but fluctuated between 4 and 5‰ at st. 1 and even dropped below 3.5‰ at st. 2 during the 1994 reproductive season. Therefore, the temporal and spatial differences in spawning observed in 1992 and 1993 can not be ascribed to salinity differences alone, although it may have been the main factor in 1994, when the low salinities demanded a greater energy input for metabolic activity.

Gamete production is correlated positively with body size and individual fecundity may be a function of population density (Levitan 1991). The densities of *M. viridis* at st. 1 increased from about 1,000 (1992), 8,000 (1993) to about 28,000 ind./m² in 1994, whereas the increase at st. 2 was much lower from about 5,000 ind./m² in 1992 to 8,000 ind./m² in 1994 (Zettler 1994). High population densities lead to a higher intraspecific competition for food and space and restricted food resources affect the gamete production. The prolongation of the development time of the gametes in 1993 and 1994 may be caused by higher densities of the animals at both stations. At st. 2, Zettler (1994) reported a general increase of the abundances of macrobenthic species since 1987, but the author could not show any significant relationships between *M. viridis* and other macrobenthic species.

Declining oxygen values and occurrence of toxic hydrogen sulphide during summer stagnation periods (2-6 mmol/l hydrogen sulphide in 1995) are the major stress factors in benthic animals colonizing shallow tideless eutrophic waters such as the DZBC (Schneider 1996). Fritzsche & von Oertzen (1995a, b) showed that *M. viridis* gradually reduces its metabolic activity as the oxygen partial pressure decreases below 20 kPa and therefore, the animals must devote a greater share of their resources in order to compensate environmental stress conditions at the expense of investment in gametes.

Changes in temperature is another important factor influencing the reproductive success. *M. viridis* spawns at water temperatures below 15°C. In laboratory studies, Bochert et al. (1996) showed that the larval development of *M. viridis* is affected by both temperature and salinity. Larvae are able to tolerate salinities below 1‰, but one-setiger larvae were unable to complete their development at salinities below 5‰. At salinities of 10 and 20‰, their development continued up to metamorphosis, when they adopted a benthic life mode. Larval development was faster at 10‰ than at 20‰, and was positively affected by higher temperatures. Moreover, the study of Bochert et al. (1996) revealed that larvae of *M. viridis*, after having reached the 4-setiger stage, are able to continue their development up to metamorphosis and adopt a benthic life in oligohaline regions where salinities do not drop below 3.5‰. This implies that st. 1 was colonized primarily by larvae that had drifted in from

more saline regions ($>5\text{‰}$). In 1994, reproduction at st. 1 was completely prevented by salinities below 3.5‰ .

Juvenile abundances exceeding $100,000 \text{ ind./m}^2$ are sometimes found in the sediment after a new generation has settled. Mortality owing to competition and lack of food can be high among juvenile *M. viridis* at this stage. This was shown by our observations during the 1992 reproductive season when good conditions for larval development led to high abundances of juveniles at st. 2. However, by the end of January, juvenile abundance has decreased to $3,000 \text{ ind./m}^2$, which was about the same as at st. 1 where the low salinity has suppressed larval development.

The ability of juvenile *M. viridis* to swim may also influence local abundances (Dauer et al. 1982). For instance, it provides a simple explanation for the doubling of the abundance to almost $7,000 \text{ ind./m}^2$ in March 1993 and the appearance of juveniles in January 1995 at st. 1. Comparing the larval abundances recorded during the three years, it is obvious that larval densities in 1993 and 1994 failed to reach the figures recorded for 1992. Relatively few animals spawned in either year, and large numbers of dead eggs were found in both. It should be emphasized that the onset, duration and end of the spawning season are all subject to variation.

In 1993, ripe animals were found over a period of two months and in large numbers ($>70\%$ of the population). This resembles the situation reported for *M. viridis* in North America (Nova Scotia) (George 1966) and the North Sea (Essink & Kleef 1993, personal observations), where almost entire populations are ripe in early January. However, these populations do not spawn in winter. Instead, the animals retain their gametes for two months until the water temperature has increased in spring.

The reproductive success of *M. viridis* in the DZBC as measured in terms of number of progeny is governed by various factors such as population density, salinity, temperature, oxygen and hydrogen sulphide levels which affect both gamete formation and larval development. During their long pelagic phase (3–12 weeks depending on the water temperature and salinity, Bochert et al. 1996), the larvae have great opportunity of dispersal. Like the adults, the larvae possess powerful physiological adaptation mechanisms which enable them to survive stress situations better than other species (Bochert et al. 1996, Fritzsche & von Oertzen 1995a, b, Schneider 1996). It is due to these factors that the species has been able to spread and colonize a wide range of habitats, especially oligohaline areas, within such a short time. In the DZBC, *M. viridis* has become an important element of the fauna and, we can be sure, has secured for itself a permanent place among the macrozoobenthos of Baltic coastal waters.

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