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MARENZELLERIA VIRIDIS (VERRILL, 1873) (POLYCHAETA: SPIONIDAE), AN INVADER IN THE BENTHIC COMMUNITY IN BALTIC COASTAL INLETS - INVESTIGATION OF REPRODUCTION

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Abstract. The reproductive biology of *Marenzelleria viridis* (Verrill, 1873) from the Darss-Zingst Bodden Chain (south coast of the Baltic) has been investigated from October 1991 to March 1993. In 1992, gametogenesis started in mid-May. The reproductive system is limited to the central region of the body. The gonads (one pair/segment) developed on the peritoneum near the metanephrides and lie ventrolaterally in the front part of each epitokal segment. All worms reached maturation simultaneously in 1992. The sex ratio was 1 : 1. Spawning occured in mid-September in 1992. Larval development was entirely pelagic. At the 3-4 setiger stage the final yolk granules had disappeared and the larvae became planktotroph. Larval growth was interrupted at the 3-setiger stage below 5 ‰. After 4 weeks the larvae reached the 16-19 setiger stage and started to metamorphose.

INTRODUCTION

The North American polychaete *Marenzelleria viridis* (Verrill, 1873) was discovered in various North Sea and Baltic Sea estuaries in the eighties (Essink & Kleef 1988, Bick & Burckhardt 1989). It was presumably imported to these coastal waters as pelagic larvae in the ballast water of ships. Bick & Burkhardt (1989) discovered the first specimens in Baltic waters in the polytrophic Darss-Zingst Bodden Chain in 1985. Since then, this spionid has become a major element of the fauna in the Bodden Chain. In 1993, 8 years after the invasion was noticed, *M. viridis* achieved biomasses of up to 800 gWW/m^2 and abundances exceeding 8,000 ind/m^2.

The worms inhabit vertical, mucus-lined burrows both in sandy (Wells & Gray 1964, Essink & Kleef 1993, Zettler *et al.*, in press) and muddy sediments (Gruszka 1991). *M. viridis* is a euryhaline polychaete, but penetrates into the oligohaline estuarine regions, forming its main distribution area in large numbers (Cowles 1931, Stickney 1959, Smith 1964, Ewing & Dauer 1982, Zettler 1993).

Some information has been published on its reproduction and larval development. George (1966) studied the reproduction of this spionid in detail. In American estuaries, gametogenesis takes place from October to March (George 1966). Pelagic larvae were found from March to May (George 1966, Simon 1968, Dauer *et al.* 1980, 1982), and juvenile benthic *M. viridis* from February to March (Boesch *et al.* 1976, Withlatch 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).

Zooplankton studies in the Boddens south of Darss-Zingst from 1987 to 1990 revealed high abundances of the pelagic larvae in autumn (Khatib 1989, Thiel 1990). The purpose of the present study was to identify the cause of this change in the reproductive period and the gametogenesis and larval development of *M. viridis*.

MATERIALS AND METHODS

The Darss-Zingst Bodden Chain is a tideless estuary on the South Coast of the Baltic. It consists of four consecutive boddens more or less linked by narrow straits (Figure 1). Salt-rich water (10 to 14 ‰) enters the Darss-Zingst Bodden Chain from the east through the narrow mouth. Freshwater is supplied to the Bodden Chain mainly by the Rivers Recknitz and Barthe. The salinity ranges from 0.5 ‰ in the western part to 14 ‰

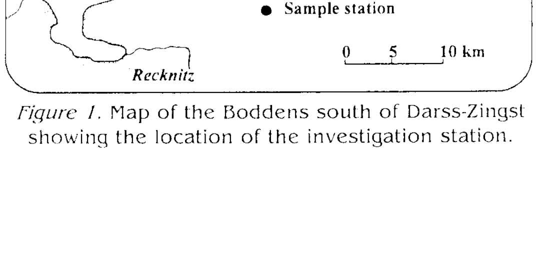

Figure 1. Map of the Boddens south of Darss-Zingst showing the location of the investigation station.

in the east. The Boddens are very shallow, the mean water depth varying between 1.5 and 2.0 m (maximum: 4.0 m).

Gametogenesis was studied by collecting adult *M. viridis* at intervals of three weeks from a station in the Darss-Zingst Bodden Chain for 12 months. The salinity at the station varied between 5.7 and 8.1 ‰ (mean: 6.9 ‰). After collection, the animals were held in 500 ml plastic vessels filled with biotope water to empty their guts. They were then stunned in sea water (10 ‰) containing 20 % $MgCl_2$ for 30 minutes and subsequently fixed in Bouin's solution. After embedding in paraffin wax, sections (3 - 5 µm) of the mid-part of the animals were produced and stained with hemalaun/eosine. The stage of gamete maturity according to Gentil *et al.* (1990) was ascertained (Table 1).

Larval development was studied by collecting plankton samples once a month outside of the reproductive period and twice a week during it. Three parallel samples were filtered through 120 µm gauze, and the numbers of *M. viridis* larvae were counted and sorted according to number of segments.

Benthos samples were taken with a corer (19.6 cm² sample area, 5 cm deep) from October to December to study the new colonization of the sediment by juvenile *M. viridis*. Three core 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 in the laboratory.

RESULTS

The gonads (one pair/segment) develop on the peritoneum near the metanephrides and lie ventrolaterally in the front part of the segment. There are none in about the first 40 and last 25 - 30 segments (Bochert 1993). In 1992, gametogenesis started in mid-May. A small number of germ cells of about 10 µm diameter (stage 1 a) were found in the gonads of some animals. It is impossible to distinguish between male and female at this stage (Figure 2).

The oogonia (stage 1 a) develop into young oocytes with a diameter of 10 -25 µm (stage 1 b) in the ovaries. The large nucleus is enclosed in a little protoplasm and

Table 1. Classification of gametes into various stages on the basis of morphological features and differentiation between male and female gametes of *M. viridis*. Modified scheme after Gentil *et al.* (1990)

Stage	Number	Morphology: Male	Morphology: Female
0	No gametes	--	--
1a	Very few gametes (not visible externally)	Small piles of germ cells (< 10 µm) on the metanephrides; males indistinguishable from females	
1b	Small numbers of gametes (not visible externally)	Accumulations of spermatogonia (5 µm) on the metanephrides	Oocytes small (10-25 µm); more or less common on the metanephride peritoneum; little protoplasm.
1c	Numerous gametes (not visible externally)	Accumulations of spermatids in the coelom; round (3-5 µm)	Oocytes isolated in parapodial space and ventral cavity near metanephrides (50-120 µm); cortical alveolis present; protoplasm plentiful; cortical layer forming
1d	Coelom completely full (visible externally)	Sperms isolated in coelom; head elongate; flagellum present	Large isolated oocytes (120-160 µm) distributed throughout the coelom; cortical layer present
2	Small numbers of gametes	A few remaining or no gametes	

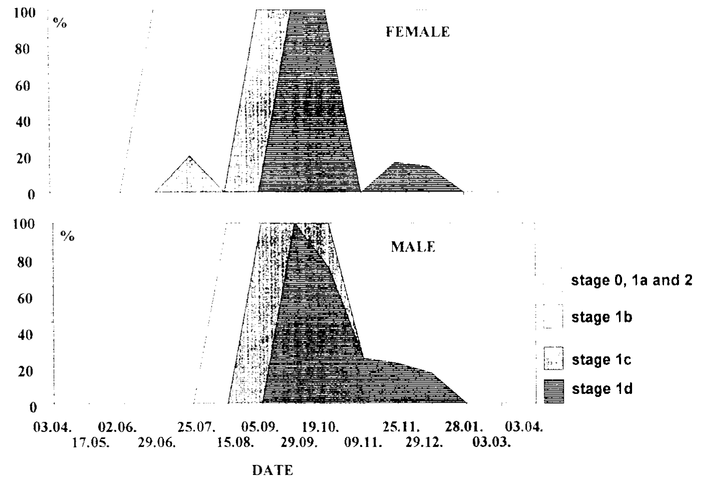

Figure 2. Development of female and male gametes in 1992/1993.

a thin egg membrane. The yolk becomes larger until the egg cells reach stage 1 c and a diameter of about 50 - 120 µm, when a few cortical alveolis can be seen in the peripheral plasma. The egg membrane changes into a radially striated cortical layer. The oocytes are released into the body cavity and parapodial space at this stage. The discus-like mature eggs with a diameter of 120 - 160 µm (stage 1 d) lie unprotected in the coelom. According to Thorson (1950), their size and little yolk indicate a pelagic larval development. Between 8 and 20 colourless, transparent alveolis can be seen in the plasma surrounding the nucleus. The oocytes are contained in a sturdy, radially striated cortical layer. The females are ready to spawn at this stage. Each female produces between 28000 and 40000 eggs.

The testes release primary spermatocytes (stage 1 a) into the coelom, where the cells lie free. Spermatogenesis is completed in the coelom. The mature spermatozoon is an ect-aquasperm according to the nomenclature of Jamieson & Rouse (1989).

Oogenesis had been completed and all females were ready to spawn in mid-September after about 17 weeks. The first male gametes (stage 1 b) could not be distinguished until mid-August (Figure 3). The duration of spermatogenesis is unknown, since it was impossible to differentiate between the early stages of male and female germ cells (stage 1 a). However, we assume that sperm development starts later. The studies published by George (1966) and Essink & Kleef (1993) yielded similar results. All males were also ready to spawn by mid-September.

Males and females can only be distinguished when mature (George 1966), but the histological sections permit reliable differentiation from early gamete development until after spawning. The sexes of all animals collected from early September to late November could therefore be determined. The sex ratio was approximately 1:1.

The worms spawned in mid-September in 1992. Gametes at stage 1 b were still found in the animals at this time. These continued to mature and refilled the coelom after spawning had taken place. Eighty per cent of all animals had spawned by the end of October. All eggs found among the plankton had been fertilized. No dead or unfertilized eggs were found. Early developmental stages (eggs, pretrochophores, trochophores) were found among the plankton in the Darss-Zingst Bodden Chain until late December. The maximum larval abundance of 21.8 million ind./m³ was observed in mid-October in 1992. The larvae reached the 16- to 19- setiger stage after a pelagic phase lasting about four weeks, and then started to metamorphose.

High abundances of early developmental stages (eggs, pretrochophores, trochophores) were again found among the plankton in mid-October, about four weeks after the first spawning, thus indicating a second spawning period. Owing to the low water temperature (below 10°C), few of this larval generation developed to

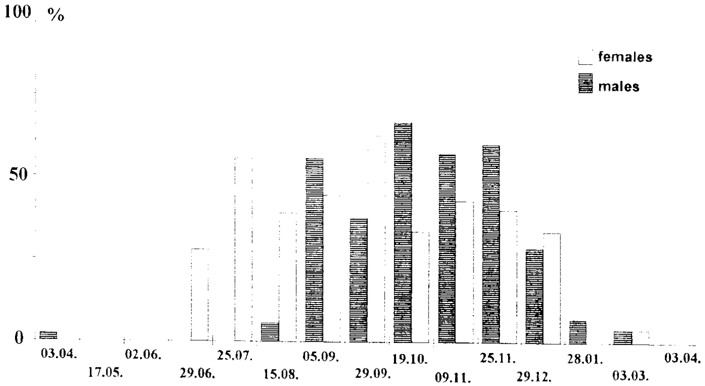

Figure 3. Percentage of male and female animals among all specimens from the Darss-Zingst Bodden Chain studied in 1992/93 (see text)

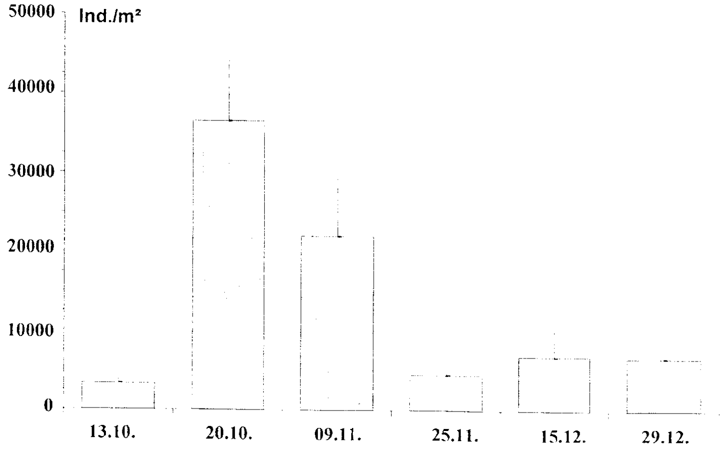

Figure 4. Abundance (+ SE) of juvenile benthic *M. viridis* with less than 50 setigers (mean value at investigation station 1992)

beyond the 6- setiger stage. A few 16- setiger larvae were found about six weeks later. The 3- setiger stage was the most common stage found in the plankton at the end of October.

According to George (1966), the planktic larvae metamorphose when they reach the 10-setiger stage. In the Darss-Zingst Bodden Chain, metamorphosis began when the 16- to 19- setiger stage had been reached, but larvae with up to 22 setigers were also often found in the plankton. The early larval development of *M. viridis* in the Bodden Chain south of Darss-Zingst Peninsula is as described by George for larvae in North American estuaries (1966).

Lateral tentacular palps develop on the peristomium when the 10- setiger stage is reached. At the 17- setiger stage, these reach to the 2nd setiger. Gastrotrochs are located behind the ciliated pit on every second setiger. The neuropodia contain hooded hooks from setiger 11 onwards.

Colonization of the sediment by juvenile benthic animals started in mid-October (Figure 4). The animals had 16 to 19 setigers. Their abundance peaked at 270000 ind./m² a week later. It then decreased and had dropped to less than 10000 ind./m² by the end of December, when juvenile benthic animals with less that 20 setigers were still found. However, by the end of December most young worms had grown to about 50 setigers.

DISCUSSION

The first specimens of *M. viridis* in the Darss-Zingst Bodden Chain were discovered in 1985 (Bick & Burckhardt 1989). The first pelagic stages were found two years later (Khatib 1989, Thiel 1990). Larval abundances reached 1 x 10⁶ ind./m³ in autumn 1989. Since then, the larvae have been found continuously in varying abundances among the plankton of these waters from September to March (Figure 5). The abundances have usually peaked in September and October, but in November in 1993. From January to March, the plankton contains only larvae with up to three setigers in 1992 and 1993. The water temperature of below 5 °C prevents the larvae from developing beyond this stage and reaching the metamorphosis stage (Bochert 1993). This observation confirms the results of George's (1966) laboratory experiments.

At temperatures above 10 °C, the pelagic phase lasts about four weeks (Bochert 1993). The larvae in the Darss-Zingst Bodden Chain was not regularly distributed. The pattern has shown patchiness by grouping closely adjacent stations according to similarity or difference in average values. This was caused by currents in the investigation area (Bochert, in press), which can distribute the larvae over wide areas during their pelagic life. Williams *et al.* (1984) showed that currents can carry pelagic larvae over distances ranging from a few tens

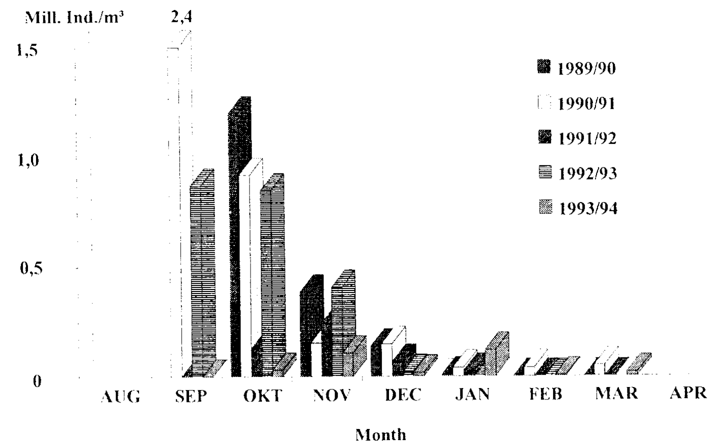

Figure 5. M. viridis larvae in the plankton of the Darss-Zingst Bodden Chain since 1989 (1989 and 1990 after Heerkloss (personal communication), 1991-1994 own data)

up to a hundred kilometres from the place where they hatched. Lagadeuc & Brylinski (1987) obtained similar results for a population of *Polydora ciliata*, the larvae of which lead a pelagic existence for five or six weeks. The long presence of *M. viridis* larvae in the plankton permitted the colonization of large areas of the Baltic Sea within a very short time. This explains the discovery of the species in the Kurian Haff (Lithuania) in 1989 by Olenin & Chubarova (1992), in the Bay of Riga in 1988 by Lagzdins (personal communication) and on the south coast of Sweden in 1990 by Persson (1991).

Results published so far show that *M. viridis* populations reproduce in spring in both North American and various North Sea estuaries (Table 2). The population in the Bodden Chain south of the Darss-Zingst Peninsula, however, reproduces already in autumn. The reason for this time lag is unclear. Differences between habitats is a possible explanation. Our investigation area is very shallow, the water warms up very fast in spring and reached temperatures of about 24°C (Figure 6) in 1992. In tidal estuaries the animals are exposed to major salinity and temperature fluctuations every few hours (Dauer *et al.* 1980, Essink & Kleef 1993). The increased energy consumption that this obviously entails might slow down the development of the gametes, which would therefore fail to reach maturity by autumn. Garwood and Olive (1978) discovered that temperature, for instance, affects oogenesis directly. By the time such temperature-stressed animals are ready to spawn, water temperatures would be so low that successful larval development would be impossible. The animals therefore spawn in spring after the water temperature has increased.

The observations of Hannerz (1956) established a more or less seasonal occurence of pelagic spionid

Table 2. Variations in the time of appearance of various developmental stages of *M. viridis* in different investigation areas (* = no data available)

Investigation area	Gametes from-to	Pelagic larvae from-to	Benthic juveniles from	Source
Lawrencetown; Nova Scotia (USA)	Nov.-Mar.	Apr.-May	*	George 1966
Chesapeake Bay; Virginia (USA)	*	*	Spring	Boesch *et al.* 1976
	*	*	Feb.-May.	Holland *et al.* 1980
	Feb.-Mar.	Feb	Mar.	Dauer *et al.* 1980, 1982
	*	*	Apr.-June	Jordan & Sutton 1984
Graet Harbor, Massachusetts (USA)	*	Ost.-Feb.	*	Simon 1968
Barnstaple Harbor, Massachusetts (USA)	*	*	Feb.-May.	Whitlach 1977
Tay Estuary (UK)	*	*	May.	Atkins *et al.* 1977
Ems Estuary (NL)	Nov.-Mar.	Mar.	May.	Essink & Kleef 1988, 1993; pers. comm.
Darss-Zingst Bodden Chain (D)	June-Nov.	Sept.-Dec.	Oct.	Present paper

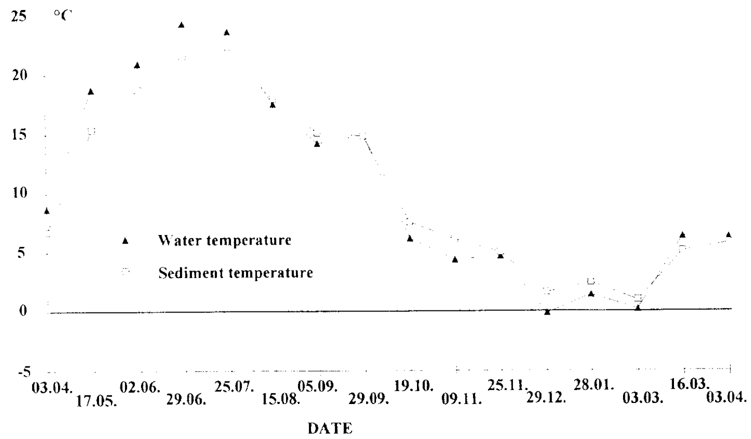

Figure 6. Water and sediment temperatures at the station during the 1992/93 investigation period

larvae throughout the year. The author found a lot of species in spring and during the period July to October. But a few species reproduced in winter. The pelagic larvae of *Scolelepis foliosa* (synonym: *Nerine foliosa*) and *Spiophanes kröyeri* were characteristic in midwinter plankton while the abundances of the larvae of *Spio martinensis* and *Laonice cirrata* decreased, like the larvae of *Marenzelleria viridis* in the Darss-Zingst Bodden Chain until the end of December. *M. viridis* doesn't reproduce at an unnormal time of year, because the results of Hannerz show, that planktotrophic development is possible during winter.

Further differences were observed in larval development and the timing of metamorphosis. In North American estuaries, the larvae change into the bottom-living form upon reaching the 10-setiger stage (George 1966), and in the Tay Estuary (Scotland) they metamorphose at the 13-setiger stage (Atkins *et al.* 1987). During our studies, metamorphosis occurred during the 16-setiger stage at the earliest.

Dean and Blake (1966) studied the larval development of *Boccardia hamata* on the North American East and West Coasts. These populations also differed with respect to the duration of the pelagic phase. Adult animals on the west coast colonize various substrates, and their larvae metamorphose at the latest when they reach the 19-setiger stage. On the East Coast, the animals are found on only a few substrates. Their larvae are very selective with regard to substrate, and their pelagic phase lasts two months, i.e. five weeks longer than that of the larvae on the West Coast. They often have up to 27 setigers. No such differences in substrate preference have been observed between the North American and the North Sea populations on the one hand, and the population in the Darss-Zingst Bodden Chain on the other.

The *M. viridis* population in the Boddens south of Darss-Zingst were ready to spawn 17 weeks after gamete development began. George (1966) studied the gamete development of *M. viridis* for 15 months. In the North American population, it began in late October. The animals were ready to spawn by the end of January, but did not actually do so until late March. Like those of George (1966), our studies show that all worms reach maturation simultaneously, and that the sex ratio is 1:1. In other words, the juvenile animals mature in less than a year. The worms do not die when spent, and it is therefore possible that they spawn several times in the course of their lives.

The onset of gamete development in mid-May, 1992, coincided with an increase in water temperature to over 20°C (Figure 6). Spawning took place after the water temperature had dropped to 15°C. Both increases and decreases in temperature are known to induce spawning (Orton 1920, George 1966). However, spawning in the Darss-Zingst Bodden Chain continued for altogether 10 weeks. The simultaneous liberation of eggs and sperm must obviously be stimulated by other factors besides the temperature during this time.

The theoretical reproduction rate is enormous. In the Darss-Zingst Bodden Chain, around 1000 females/m^2 (mean abundance: 2000 ind./m^2, sex ratio 1:1) are able to produce about $30 \cdot 10^6$ eggs/m^3 (personal observation). However, in 1992 not more than 1.0 % (270000 juvenile worms/m^2) reached the benthic juvenile stage.

The benthic juveniles of *M. viridis* are highly mobile (Dauer *et al.* 1980, 1982). In March 1993 Schmidt & Schaarschmidt (personal communication) found large numbers of juvenile worms with about 50 setigers in the near surface plankton. A further migration into the Darss Zingst Bodden Chain took place in this way during the spring of 1993, i.e. the species does not spread only in the form of planktic larvae, but also as benthic juvenile worms.

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