

Population dynamics, growth and production of the neozoon *Marenzelleria* cf. *viridis* (Verrill, 1873) (Polychaeta: Spionidae) in a coastal water of the southern Baltic Sea

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Abstract

The propagation of an immigrant from North America, viz. the spionid *Marenzelleria* cf. *viridis* in the Darss-Zingst Bodden (DZB) (southern Baltic Sea), was studied at three stations from March 1992 to December 1995. Highest mean abundances (over 28 000 ind. m⁻²) and wet weights (400 g m⁻²) were recorded at station 2 in 1994. The spionid also reached its highest dominances in terms of biomass (40 to 90%) at this station, which was selected for the population dynamics, growth and secondary production studies. The spionid has a life span of about 3 years, and many individuals achieved sexual maturity after one year. Their growth curve is steepest during the first year of life, during which the animals grow to a length of about 180 segments. However, growth depression was observed during the ripening of the gametes in April, May and June. Secondary production was in the region of 55 to 85 g AFDW m⁻² y⁻¹. Productivity (P/B) varied considerably from generation to generation, ranging between 0 and 4.8 with an average between 1.2 and 1.6.

Introduction

The immigration and/or introduction of new species into existing communities is an important event both in terrestrial and aquatic biotopes focussing interest on consequences for the indigenous flora and fauna and the possibility of economic benefits or damage. The main risks associated with invasion by new species include degradation of the host environment, destruction of existing communities, genetic influences and the introduction of diseases and parasites (Carlton & Geller, 1993; Hedgpeth, 1980; Reise, 1993). Many species now established in European waters have immigrated in the course of the past century, the best known being *Dreissena polymorpha* (Mollusca), *Orconectes limosus* (Crustacea), *Cordylophora caspia* (Hydrozoa) and the muskrat *Ondatra zibethica*. So far over 30 'exotic' species have immigrated to or have been accidentally introduced in the North Sea and Baltic Sea (Jansson, 1994; Leppäkoski, 1984, 1991; Reise, 1993). The more recent of these immigrants include

the amphipod *Gammarus trigrinus* and the polychaete *Marenzelleria* cf. *viridis* (e.g., Zettler, 1995; Zettler, 1996a).

This paper presents the results of a four year study into the population dynamics, growth and production of a North American spionid, *M.* cf. *viridis*, originally identified as *Marenzelleria viridis* (Verrill, 1873) (syn. *Scolecopides viridis*) in a coastal water of the southern Baltic Sea. The original area of distribution of *M.* cf. *viridis* is the North American east coast between 32 and 60° N (Zettler et al., 1995). The present contribution deals with the biology of the neozoon and compares it with that of populations in its areas of origin and immigration.

Materials and methods

Ecological field studies were performed in the Darss-Zingst Bodden (DZB), a coastal water of the southern Baltic Sea, located 20 to 30 kilometres north east of

Table 1. Range of annual means (monthly measurements) of selected abiotic parameters at stations 1 to 3 during 1992–1995

Station 1	stn. 1	stn. 2	stn. 3
Temperature (°C)	9.8–11.8	8.2–10.5	8.8–10.9
Salinity (PSU)	6.6–9.8	2.6–5.4	5.4–8.0
Sediment:			
Water content (%)	22.6–23.8	27.7–30.3	27.5–28.4
Organic content (%)	0.49–0.56	1.07–1.42	0.75–1.19
Mean grain size (µm)	255–279	271–305	214–293
Fraction < 63 µm (%)	1.28–1.81	2.81–3.42	1.97–3.74

Rostock (54°20' N; 12°30' E) and measuring about 40 km in length from West to East. Variations in abundance and biomass were studied at three stations that differed in abiotic parameters (Table 1). The investigation area and methods are more closely described in Bastrop et al. (1997) and Zettler (1996a). The population dynamics, growth and production of this population will be described using station 2 as an example.

Benthos samples were taken with a 78.5 cm² cross section corer to a depth of 40 cm. At three stations 3 cores were collected at monthly intervals, sieved over 0.3 mm meshes (top 10 cm of the sediment) and 0.5 mm meshes (10 to 40 cm depth) and then fixed in 4% borax-buffered formalin. The smaller of the two meshes ensured that all juvenile *M. cf. viridis*, which penetrate only a few centimetres into the sediment, were recovered. Only larger *M. cf. viridis* and *H. diversicolor* individuals, in contrast, burrow more than 10 centimetres into the sediment, so that the 0.5 mesh was chosen to separate the animals from the sediment without unnecessary destruction (see also Zettler et al., 1994). The abundances of species were calculated as means ± SD per m². In addition, at each sampling station the top layer (5 cm) from an additional one corer was taken for analysis of sediment parameters. The biomass of each species was determined and expressed as wet weight (± 0.1 mg) m⁻².

The maximum width between the 5th and 10th segment of all *M. cf. viridis* found in the samples was measured to permit identification of the different generations and subsequent cohort analysis. Each month intact animals from station 2 were used to calculate regression formulae between width and segment number, width and length, and width and individual wet weight (IWW) (Figure 1). In all regressions, the power function had the highest degree of determinacy.

Crisp's (1971) method was used to estimate the production of *M. cf. viridis*. Width – IWW regression

was used to calculate a mean biomass and production per generation and month. The monthly production values were added to obtain the annual production. Conversion of wet weight (WW) to ash-free dry weight (AFDW) was based on regression obtained from 25 measurements (Figure 2). Production was estimated for the year classes 1992/93, 1993/94 and 1994/95 only at station 2, starting at the time of recruitment (October/November) in each year.

Results

Abundance and biomass

Figure 3 presents the annual mean abundances and biomasses of *M. cf. viridis* at stations 1 to 3. Numerical densities varied distinctly from station to station and from year to year. At station 1 ($S = 6–8$ PSU) the annual mean abundance increased only slightly from 1992 to 1994/95, rising from 5000 ind. m⁻² to 8000 ind. m⁻². The highest annual mean wet weight (over 400 g m⁻²) was measured in 1993–1994.

At station 2 ($S = 2–4$ PSU) densities increased from approx. 2000 ind. m⁻² in 1992 to over 28 000 ind. m⁻² in 1994 (Figure 3). By 1995, the population density had decreased again to about 4000 ind. m⁻², i.e., only slightly above the initial value recorded in 1992. The biomass also reached its highest values in 1993–1994, the wet weight increasing from ca. 100 g m⁻² in 1992 to over 300 g m⁻² in the following year, but then decreasing again in 1995 to 250 g m⁻².

At station 3 ($S = 4–6$ PSU) densities remained ca. 2000 ind. m⁻² (Figure 3). The mean annual wet weight at this station decreased from 280 g m⁻² in 1992 to 120 g m⁻² in 1995.

Individual and biomass dominance

The dominant taxa making up ca. 90% or more of the total density at stations 1–3 are shown in Table 2. Altogether, 25 taxa were found.

Station 1 (23 taxa) exhibited the greatest species diversity. Here *M. cf. viridis* achieved a dominance of 32–52% in terms of individuals and of 66–80% in terms of biomass (Table 3). *Hydrobia ventrosa* achieved relative abundances of 16–29%. In terms of biomass, only the nereid *Hediste diversicolor* achieved a comparable abundance of 20–30%.

With only 12 taxa, station 2 was the one with the lowest number of species. Only *M. cf. viridis*

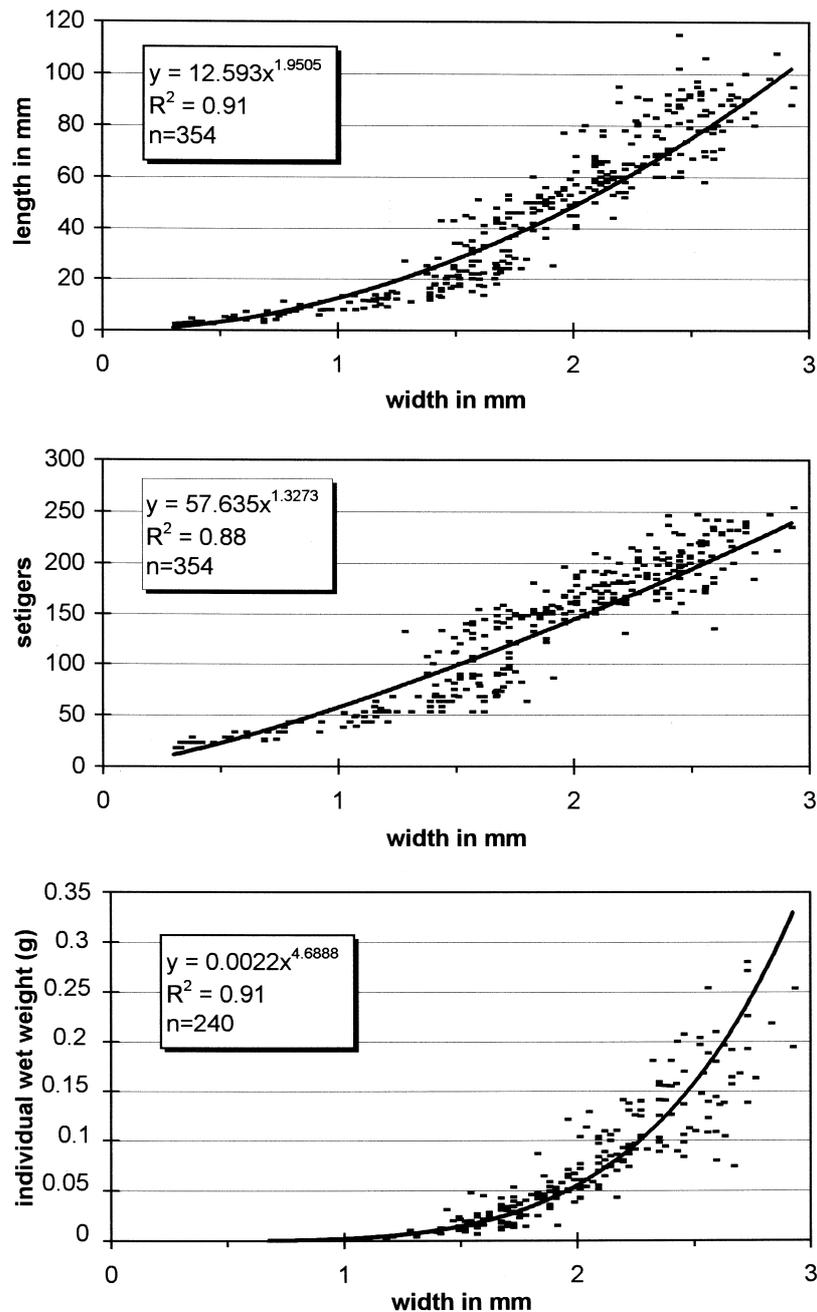


Figure 1. Regression between body width (between segment 5 and 10) and length, number of segments (setigers) and individual wet weight (IWW) of *Marenzelleria cf. viridis* at station 2.

and chironomids were really dominant. The individual dominance of the sponiid varied between 37 and 92% (Table 2). Dominance among the chironomids fluctuated correspondingly between 7% and 56%. In terms

of biomass, however, the station was clearly dominated by *M. cf. viridis* (92–96%) (Table 3).

Station 3 with its 18 taxa occupied a median position. *M. cf. viridis* was the most dominant species only in 1992 (40%) and 1994 (31%). The dominant spe-

Table 2. Relative abundance (%) of the dominant taxa at stations 1 to 3, total abundance (ind./m⁻²) of all taxa found (annual means)

	Station 1				Station 2				Station 3			
	1992	1993	1994	1995	1992	1993	1994	1995	1992	1993	1994	1995
<i>Hydrobia ventrosa</i>	29	29	20	16	0	0	0	0	3	3	25	8
<i>Hediste diversicolor</i>	11	12	9	11	0	0	0	0	29	15	25	44
<i>Marenzelleria cf. viridis</i>	32	40	52	49	49	74	92	37	40	20	31	33
<i>Tubifex costatus</i>	10	6	11	9	1	1	0	2	0	0	0	0
<i>Corophium volutator</i>	12	8	0	0	0	0	0	0	24	59	10	0
Chironomidae	0	0	0	2	50	25	7	56	0	0	2	2
Total (%)	94	95	92	87	100	100	99	95	96	97	93	87
Total (ind./m ⁻²)	14464	15557	16255	17569	4915	10860	29887	10205	8609	14834	6937	6555

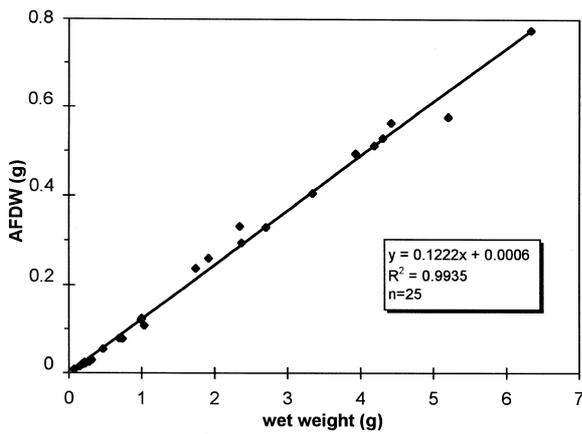


Figure 2. Regression between wet weight and ash-free dry weight (AFDW) for *Marenzelleria cf. viridis*.

Table 3. Proportion (%) of *Marenzelleria cf. viridis* in the total biomass from 1992 to 1995

	1992	1993	1994	1995
Station 1	80	68	71	66
Station 2	92	93	96	93
Station 3	72	65	52	38

cies in 1993 was *Corophium volutator* (59%) and in 1995 *Hediste diversicolor* (44%). The dominance of *M. cf. viridis* in terms of biomass decreased from 72% in 1992 to 38% in 1995 (Table 3), the relative biomass of *H. diversicolor* increasing from 30% to 60% during the same period.

Population dynamics

Figure 4 shows the size frequency distribution and occurrence of four generations of *M. cf. viridis* revealed

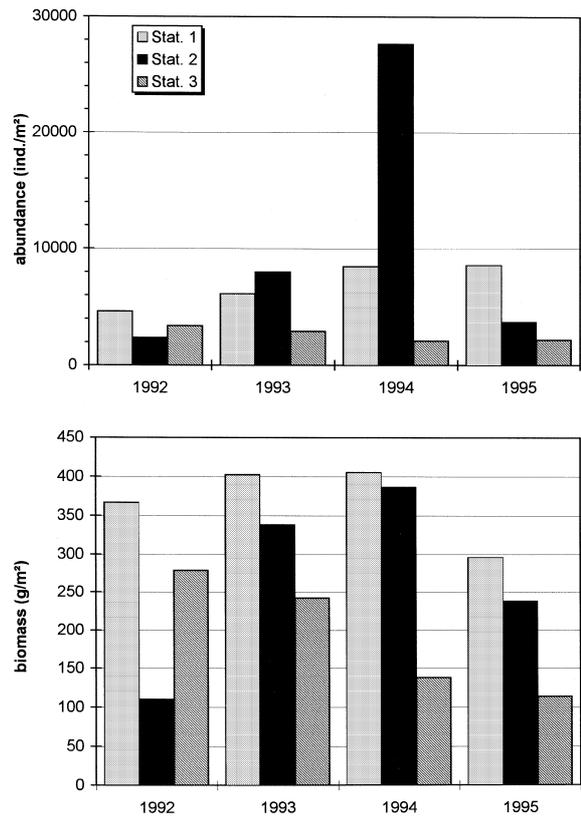


Figure 3. Development of mean annual abundance (ind. m⁻²) and mean annual biomass (g wet weight m⁻²) of *Marenzelleria cf. viridis* at stations 1 to 3 from 1992 to 1995.

by cohort analysis on the basis of body width. Two or three generations could be observed simultaneously. The ‘recruitment community’ of each year, i.e., all animals that colonized the benthos as planktic larvae during a single reproduction phase of three months, was regarded as one generation (F1, F2, F3 and F4). Within a population, the year classes differed with

respect to length, number of segments and width. These differences became less as the generations aged (after about 1.5 to 2 years), so that, in addition, the number of gill-bearing segments was used for reliable differentiation between generations within size classes. In animals aged 2 years and more gill appendages are found on over 60 segments, whereas animals of year class 1 have only 40–50. As no such differentiation was undertaken at the beginning of 1992, the F1 generation consists of animals ‘born’ in 1990 and 1991.

Reproductive success at station 2 was greatest in 1992 and 1993 (Figure 5). The mean density of the F1 generation ranged from a few 100 ind. m^{-2} to 2000 ind. m^{-2} , whereas in autumn 1992 mean densities of around 4000 ind. m^{-2} were recorded for the F2 generation. The last animals of the F2 generation were found in August 1995, i.e. almost 3 years later. Extremely successful reproduction in autumn 1993, caused F3 generation abundance of over 50 000 ind. m^{-2} , but this had declined to about 10 000 ind. m^{-2} by the end of 1994. Reproduction was virtually zero at station 2 in 1994 and 1995 (Figures 4 and 5). In 1995, however, a few F4 generation individuals were found four months after the reproduction season; these must have reached the station by active or passive migration. The density of the F4 generation was only a few 10 ind. m^{-2} to 100 ind. m^{-2} . No sign of an F5 generation was found at station 2. Generations F2 and F3 differ by a whole width class of 0.4 mm in March 1993 and March 1994 (Figure 4). This corresponds to a difference in length of 30 segments. Figure 4 (see March 1992) also clearly shows that reproduction and settlement must have been low in 1991 as well, so the F1 generation at this station may have been a more or less uniform year class (1990) after all. This seems quite likely as *M. cf. viridis* first colonized this station in 1990 and, consequently, there can not have been any earlier year class.

Growth

Growth varied in both space (from one station to another) and time (from one year to another). This is best seen when the increase in length and segment number is largest, i.e. during the first year of life. Once again, station 2 is used to describe the general growth pattern of *Marenzelleria cf. viridis*. When settlement begins in October (=day 0) the average animal has 15 to 20 segments (Figure 6). The steepest growth at station 2 was observed in 1992–1993, when the animals grew to an average of 80 segments within 100 days. Growth

Table 4. Secondary production (in g AFDW) of *Marenzelleria cf. viridis* from 1992 to 1995 broken down by generations F1 to F4; calculated according to Crisp (1971)

	1992–1993	1993–1994	1994–1995
F1	–4.34	–3.8	–
F2	59.82	4.28	5.96
F3	–	85.81	48.39
F4	–	–	0.31
Total	55.48	86.29	54.67

was somewhat slower from March to June (day 120 to 220), but increased again in summer and autumn until the animals had grown to about 180 segments. The 1993–1994 generation grew less rapidly, and two depressions were observed in the growth rate. Growth slowed down in February (day 100) and then ceased until May (day 170), when growth was resumed until the animals had reached a length of 100 segments in July (day 260). Growth was then interrupted again until September (day 310) when renewed growth brought the animals to a length of 110 segments in late autumn. Thus, this generation of *M. cf. viridis* remained about 70 segments shorter than that of the previous year. These two growth curves for *M. cf. viridis* at station 2 represent two extremes, the growth curves found at the other two stations lying in between (Zettler, 1996b).

Production

The production data calculated for the various generations of *M. cf. viridis* at station 2 are presented in Table 4. These data show clearly the interannual variations and differences between year classes (generations F1 to F4). ‘Negative’ production was caused by a decrease in abundance and biomass during the year. The major part of production in 1993–1994 (85 g AFDW m^{-2}) did not stem from the newly settled F4 generation (failed reproduction), but resulted from previous years’ F3 generation. Total annual production, however, was about the same in each of the years. The production/biomass ratio (P/B) also shows different values for the various generations (0–4.76). P/B ratios calculated from the total and annual data vary less, ranging between 1.17 and 1.56.

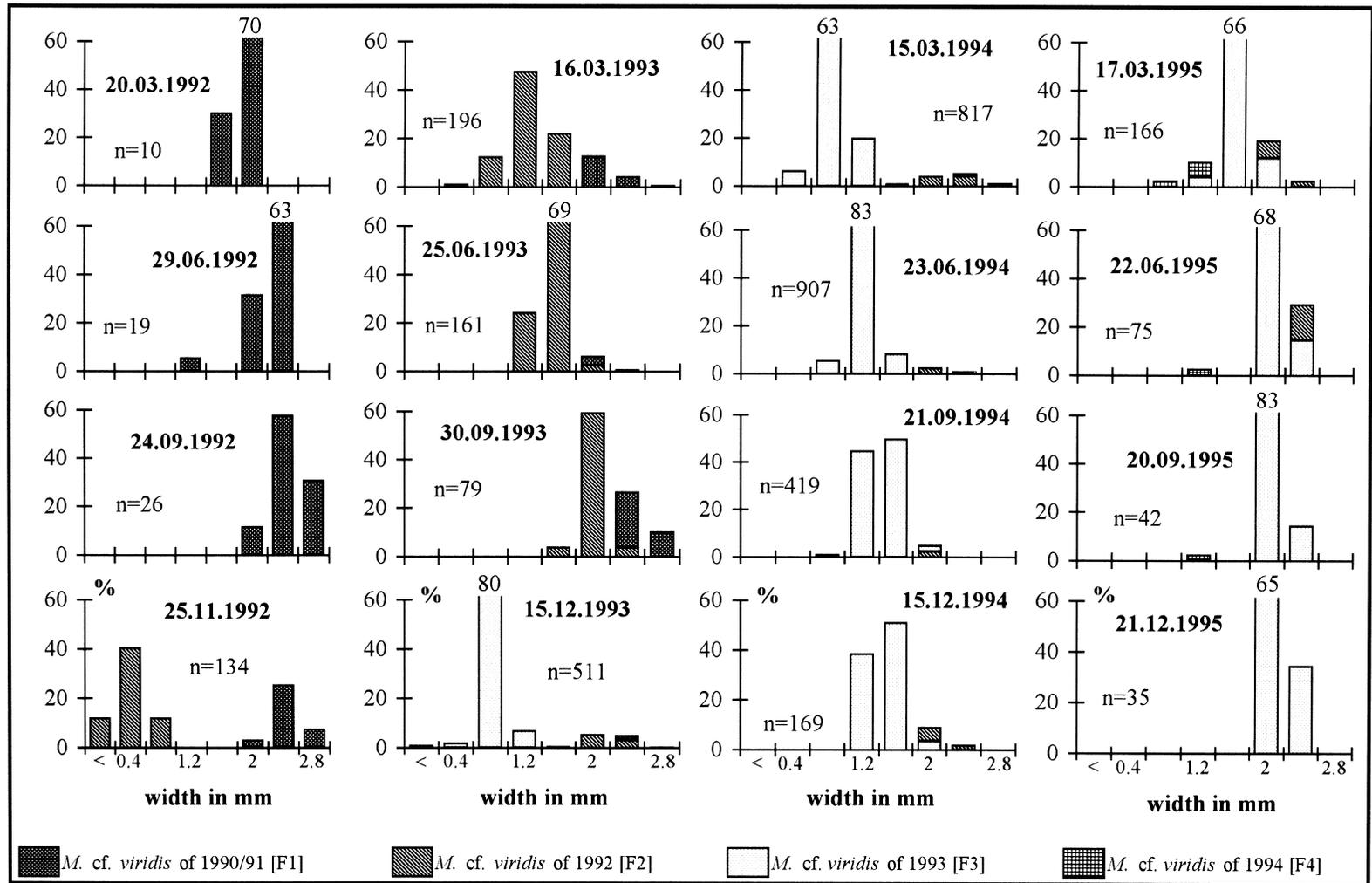


Figure 4. Population dynamics of *Marenzelleria cf. viridis* at station 2 from 1992 to 1995 broken down by generations F1 to F4 as measured by means of the body width between segments 5 and 10.

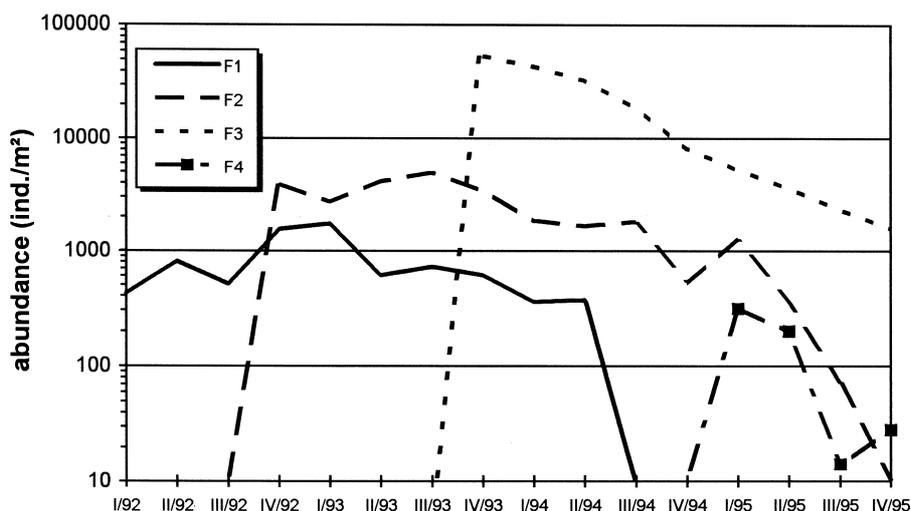


Figure 5. Variation in the abundance (ind. m^{-2}) of *Marenzelleria cf. viridis* at station 2 from 1992 to 1995 broken down by generation (F1 to F4); quartals I to IV give the means for three months (e.g., I/94 = mean for January, February and March 1994).

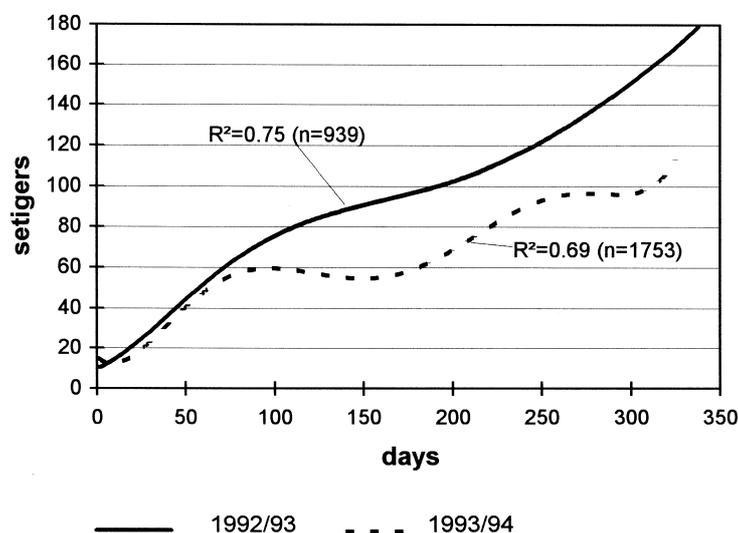


Figure 6. Growth curves for *Marenzelleria cf. viridis* during their first year of life (1992–1993 and 1993–1994) at station 2. R^2 =coefficient of regression, n =number of measured individuals, Number of setigers converted from body width.

Discussion

Population dynamics

In the Darss-Zingst Bodden, mean annual abundances of *M. cf. viridis* varied between 1000 ind. m^{-2} and 28 000 ind. m^{-2} . Higher densities (up to 250 000 ind. m^{-2}) were found during recruitment periods (Zettler et al., 1995). The dominance of the species (individuals and biomass) in this estuary with its relatively low species diversity ranges between 40% and

90%. Similar findings have been reported for Georgia (USA) by Dörjes & Howard (1975). In oligohaline regions salinity has a clear impact on recruitment. Reproductive success was recorded at all stations up to 1994, but at station 2 reproduction failed as soon as the salinity dropped below the 5 PSU limit. Although adults from previous generations were still found in the area, no new generations appeared. As a consequence, the population density dropped from its maximum of almost 60 000 ind. m^{-2} in 1994 to only a few 1000 ind. m^{-2} in 1995 (see also Zettler 1996b). Appar-

ently, juvenile and adult *M. cf. viridis* are quite able to colonize oligohaline regions, but not to metamorphose from egg through larva to benthic juvenile or to achieve full sexual maturity there (Bochert & Bick, 1995; Bochert et al., 1996; George, 1966). This potential for colonizing oligohaline waters is also reflected in a high tolerance to low salinities. Fritzsche (1995) showed that larval, juvenile and adult *M. cf. viridis* can survive salinities < 1 PSU for over 48 h and that, as the animals develop, this tolerance increases significantly from 0.77 ± 0.2 PSU (for larvae with 1–3 segments) to 0.03 ± 0.03 PSU (for adults). Adult *M. cf. viridis* are thus able to penetrate even into the limnic parts of estuaries.

Owing to its life span of about three years and its tolerance of low salinities, *M. cf. viridis* is quite capable of surviving in waters with aperiodic phases (1 to 2 years) of salinities < 5 PSU by waiting for conditions that are more favourable for reproduction. Animals reproduce after their first year of life, so that an individual can reproduce two or three times during its life. In the DZB, gametal development began in mid-May, and the gametes became ripe in late September (Bochert & Bick, 1995). Spawning took place from mid-October to mid-January. The life span of *M. cf. viridis*, however, seems to depend strongly on external conditions. In the DZB it differed by only three months between stations, but life spans reported in the literature differ considerably. Sarda et al. (1995b), for instance, give a life span of 9–14 months for a North American *Marenzelleria* population, stating that sexual maturity is reached after only four months. Essink & Kleef (1993) mention that several generations exist concurrently and that the life span is longer than one year. Atkins et al. (1987) give no information on age, but observed reproductive success only once in three years, thereby implying a longer life span. George (1966) concluded from the synchrony of maturity in all animals that *M. viridis* achieves sexual maturity within a year. The life span of about 3 years of *M. cf. viridis* is much longer than the average of 1 to 2 years reported for other spionids, e.g., *Spio*, *Polydora*, *Pygospio*, *Prionospio* and *Streblospio* (Ambroggi, 1990; Gudmundsson, 1985; Lambeck & Valentijn, 1987; Sarda et al., 1995b). For *Malacoceros fuliginosus*, however, a life span exceeding 2 years has also been reported (Gudmundsson, 1985). This species reaches sexual maturity in less than a year.

Growth and production

M. cf. viridis grows very quickly during its first year of life. With a maximum segment number of about 250, this spionid reached 50–70% (110–180 segments) of the ultimate number after only 350 days. This corresponds to a length of about 70 mm and a wet weight of up to 0.15 g. This period of intensive growth is not continuous, however. Reduced growth does not occur in winter as one might expect, but partly in April/May/June as the water temperature increases. This period coincides with the commencement of gametal development (Bochert & Bick, 1995). The energy needed to begin gametal development is possibly so high that growth is impossible at this point. Growth is not resumed until the water temperature is about 10 °C. Temporal variations in growth cannot easily be attributed to temperature variations; they are more probably linked to differences in population density and food availability (see also Sarda et al., 1995b).

The capacity for growth is reflected in the production and productivity (P/B) of the youngest generation in each year. The rapid growth of *M. cf. viridis* is linked to its achievement of sexual maturity and participation in reproduction after only one year (Bochert & Bick, 1995). Sarda et al. (1995b) and George (1966) also saw similarly rapid maturation in North American populations. It should be noted, however, that Sarda et al. (1995b) reported a life span of only 14 months for *M. viridis* in North America. These authors reported the highest P/B ratio known for polychaetes for *M. viridis* colonizing an area previously cleared of fauna by ice (Table 5). On the other hand, they analyzed the production and growth of only one year class at that time ($P = 60 \text{ g DW m}^{-2} \text{ y}^{-1}$; $P/B = 6.1$) and found that production in the following year was only one third as high ($P = 26.3 \text{ g DW m}^{-2} \text{ y}^{-1}$; $P/B = 4.5$), possibly due to increased competition for food and predation pressure.

M. cf. viridis in the DZB achieved the highest production ever reported for polychaetes (Table 5), but, with $P/B = 1.2$ to 1.6, its productivity was lower than reported elsewhere owing to the relatively high biomasses of between 29.6 and 53 g AFDW m^{-2} . It should be noted that when the generations are considered separately, the youngest generation accounted for the largest contribution to growth and, thus, to annual production, except in 1994–1995 (Table 4). The P/B ratio of 4.8 for the F3 generation in 1993–1994 is therefore fully consistent with the above results. This shows once again quite clearly the importance of considering

Table 5. Various estimates of polychaete production (P) in dry weight (DW in $\text{g m}^{-2} \text{y}^{-1}$) and ash-free dry weight (AFDW in $\text{g m}^{-2} \text{y}^{-1}$); P/B = ratio of production and biomass

Species	P	P	P/B	Author
<i>Arenicola marina</i>	9.1		0.7	Wolff & De Wolf (1977)
<i>Nephtys hombergi</i>		0.04–0.2	0.9–2.3	Elliott & Taylor (1989)
<i>Marenzelleria cf. viridis</i>	67–107	55–86	1.2–1.6	this paper
<i>Polydora quadrilobata</i>		02–2.6	1.8–8.2	Lambeck & Valentijn (1987)
<i>Hediste diversicolor</i>	61		2.5	Heip & Herman (1979)
<i>Nereis virens</i>		23.7	2.5	Kristensen (1984)
<i>Streblospio benedicti</i>	0.9–1.7		2.5–2.8	Sarda et al. (1995a)
<i>Hediste diversicolor</i>		27.2	2.6	Kristensen (1984)
<i>Hediste diversicolor</i>	12.8		3.0	Chambers & Milne (1975)
<i>Polydora ligni</i>	0.86		3.06	Sarda et al. (1995b)
<i>Capitella capitata</i>	0.38–1.6		3.3–11.6	Oynekam (1983)
<i>Prionospio caspersi</i>			4.09	Ambrogi (1990)
<i>Streblospio shrubsoli</i>	15.7		4.4	Sarda & Martin (1993)
<i>Marenzelleria viridis</i>	60		6.1	Sarda et al. (1995b)

the generations separately when estimating production and emphasizes the problem of making such estimations for species with life spans of more than one year (see also Elliott & Taylor, 1989). Lambeck & Valentijn (1987) also underlined the importance of considering the life span of polychaetes when estimating production. Relatively high P/B ratios can be expected in small species with a life span of one or two years (e.g. *Capitella capitata*; P/B = 3.3–11.6). P/B ratios between 2.5 and 3 have been reported for *Hediste diversicolor*, which has a life span of 3 or more years. Larger polychaetes having a high biomass and a life span of three years and more such as *Arenicola marina* and *Nephtys hombergi* have a P/B ratio of about 1 (see Table 5 for references).

Altogether, it can be stated that the immigration of *M. cf. viridis* into the DZB has increased local zoobenthic production ten-fold. Arndt (1994) reported a macrozoobenthic production of $9.4 \text{ g DW m}^{-2} \text{y}^{-1}$ (about $7.4 \text{ g AFDW m}^{-2} \text{y}^{-1}$) before 1980. In 1992, *M. cf. viridis* alone accounted for a secondary production of $1.47\text{--}21.65 \text{ g org. C m}^{-2} \text{y}^{-1}$ (about $2.5\text{--}36 \text{ g AFDW m}^{-2} \text{y}^{-1}$) (Arndt, 1994). These estimates, however, are based only on the biomass measured and do not take the generation cycles of the taxa into account. Nevertheless, *M. cf. viridis* has become one of the most important representatives of the macrozoobenthos in terms of production only a few years after its immigration. Between 1992 and 1995 the production of *M. cf. viridis* amounted to $55\text{--}86 \text{ g AFDW m}^{-2} \text{y}^{-1}$. These results confirm the role of

this spionid as an opportunistic species that is able to colonize new habitats explosively and prepare them for colonization by other organisms (Reinharz, 1983; Sarda et al., 1995b). On the other hand, owing to its relatively long life span, *M. cf. viridis* is also very well able to survive periods of suboptimal conditions (e.g. low salinities).

In view of what we know so far, *Marenzelleria cf. viridis* appears to have found a niche in Baltic eutrophic brackish waters and will probably remain part of the community.

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