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Species Strategy Near Its Boundary: the *Marenzelleria* cf. *viridis* (Polychaeta, Spionidae) Case in the South-Eastern Baltic Sea

key words: life cycle, reproduction, colonisation, oogenesis, salinity

Abstract

The invasive polychaete worm *Marenzelleria* cf. *viridis* spread into various coastal habitats in the Baltic Sea. The estimated limits regarding its salinity tolerance obtained from different laboratory experiments alone only rarely explain the actual species boundaries in nature, e.g. in the Curonian lagoon. Therefore, a field study was carried out aimed at to define, how a population maintains itself in a dynamic estuarine habitat with rapid and irregular changing salinity (annual mean 3 PSU, range of variation from 0 to 7.5 PSU). Under these conditions the species females reached maturity. However, during the final reproduction phase their spawning was delayed and oosorption started. It was estimated that roughly 0.05% of the nearby sea population offspring was transported to the estuary but most of the pelagic larvae were not able to develop beyond the 10 segments stage. It seems that the estuarine benthic population is maintained by migration of the species benthic stages. This mode probably is more efficient in comparison to dispersal by pelagic larvae when a species colonises stressed and dynamic environments.

1. Introduction

The introduction of the brackish water polychaete *Marenzelleria* cf. *viridis* into the Baltic Sea is a good example for the expansion course of a non indigenous species. Although *M. cf. viridis* has spread within the Baltic Sea, it was not able to colonise the deeper parts below 50–60 m depth (ZMUDZINSKI *et al.*, 1997; OLENIN and CHUBAROVA, 1994) and numbers decreased rapidly with increasing distance from the shore (KUBE *et al.*, 1996; KUBE and POWILLEIT, 1997). On the other hand, it settled very successfully in various shallow oligohaline areas (Darss-Zingst Bodden Chain: ZETTLER, 1996; Curonian lagoon: DAUNYS and OLENIN, 1999; Gulf of Riga: CEDERWALL and JERMAKOV, 1999; southern coast of Finland: NORKKO *et al.*, 1995).

Numerous experiments performed on *M. cf. viridis* revealed, that this species is well adapted to cope with short-term hypoxia and appearance of hydrogen sulphide (BOCHERT *et al.*, 1997; SCHIEDEK, 1997; HAHLEBECK *et al.*, 2000). Salinity tolerance of adults is extended down to 0.03 PSU, though generally the species reproduction is limited by salinity lower than 5 PSU (BOCHERT *et al.*, 1996b; FRITZSCHE, 1997).

In the coastal waters off Lithuania (salinity 7–8 PSU) (Fig. 1), mean densities of *M. cf. viridis* vary from 1000 ind/m² in the shallow sandy areas above 20 m depth down to 250 ind/m² in depths below 20 m (Van Veen grab samples). The estuarine *M. cf. viridis* population in the Curonian lagoon has a relatively low density (250 ind/m² – core samples) and is distributed within the area affected by seawater inflows (annual average from 3.6 down to 0.2 PSU). The species is present there since its invasion in 1990 (OLENIN and

CHUBAROVA, 1994; ZMUDZINSKI *et al.*, 1997; own observations), but similar to other euryhaline species it does not settle in the part of the estuary with permanent freshwater conditions.

The estimated limits from the above mentioned laboratory experiments alone only rarely explain the actual species boundaries in nature, *e.g.* in the Curonian lagoon, since the majority of such development and/or tolerance experiments were carried out at steady-state laboratory conditions. Range and frequency of factor fluctuations may be much more important determinants of biotic response in the dynamic environments, where pulse events are common (RICHMOND and WOODIN, 1996). Consequently, the species actual distribution in a stressed ecosystem will not be completely understood as long as the population strategy in marginal areas is not known.

The aim of this study, therefore, was to define how *M. cf. viridis* population is maintained in an estuarine habitat with freshwater to oligohaline conditions, where rapid and irregular salinity changes occur. We addressed this question using observations on success of i) benthic population during late reproduction period; ii) pelagic larvae development and iii) the following recruitment.

2. Material and Methods

2.1. Study Area

The Curonian lagoon is a shallow transitory brackish-to-fresh water body separated from the southeastern Baltic Sea by a narrow spit (Fig. 1). The mean depth of the lagoon is 3.8 m. Bottom sediments are mainly formed of well sorted thin-grained sand ($Md = 0.18$) (GULBINSKAS, 1994). Recent annual sedimentation rate is about 3.2 mm (PUSTELNIKOVAS, 1995). Content of organic carbon in the sediment is 1.8% in the northern part and increases towards the sea up to 3.8–11.8% (GUDELIS and PUSTELNIKOVAS, 1983). At the sampling site where this study was carried out the organic content in the sediment was 1.2 ± 0.28 between June and October (measured as loss on ignition).

Since the lagoon is a transition area between the river Nemunas and the Baltic Sea, many environmental characteristics, which are coupled with the current hydrological condition, show great variations. Mean annual salinity values are between 7 and 8 PSU in the open sea, but decrease down to 3.6 PSU in the lagoon mouth area and reach a minimum of approximately 0.01 PSU in the area of the freshwater runoff. Sudden salinity changes from almost freshwater conditions up to 8 PSU are common in the lagoon, but show no specific exchange patterns on short-time scales (Fig. 2a).

Long-term salinity data show that during spring and winter seasons monthly average values are low (1.5–3.0 PSU) due to prevailed freshwater runoff conditions in the lagoon (Fig. 2b). However, during summer and autumn frequency and volume of inflows from the sea increased significantly (GAILIUŠIS *et al.*, 1996) followed by a salinity rise up to 3.0–4.5 PSU. In the year this study took place (1996) mean annual salinity was nearly 3 PSU (not published data from Marine Research Centre, Klaipėda). In October and November average salinity values (>5 PSU) were significantly higher than the long-term monthly average for the same period (means calculated from daily salinity values, Fig. 2a, b).

The wind-caused occasional rise of water level in the coastal zone of the sea has an effect on both duration and extent of the seawater intrusions (ŽAROMSKIS, 1996). The total water volume transported annually from the sea into the lagoon appears to be equal to the total volume of the lagoon ($\sim 6 \text{ km}^3$), whereas freshwater runoff exceeds this amount approximately 6 times (GAILIUŠIS *et al.*, 1996).

According to long-term data, water temperature starts to increase at the end of April and reaches values between 10.5 and 14.0 °C in the middle of May (JUREVIČIUS, 1959; DUBRA, 1995). During the summer months as well as in early autumn the temperature reaches 18.8–22.7 °C. In 1994–1996 the ice covering began in December and melting was observed during February–March (DUBRA, 1995).

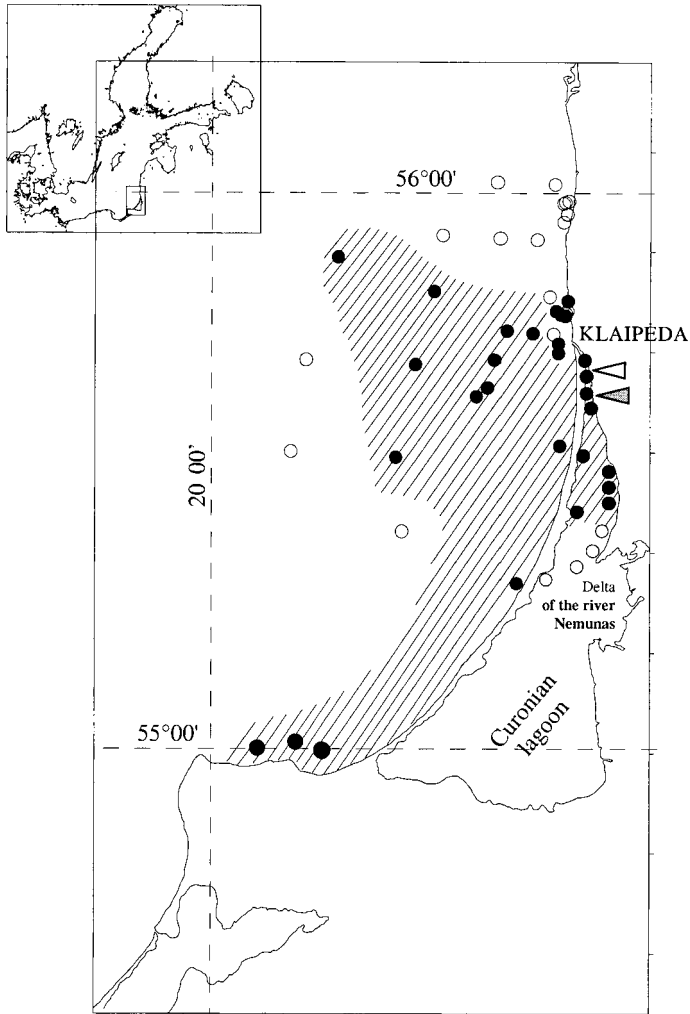


Figure 1. Study area in the south-eastern Baltic Sea and habitats colonised by *Marenzelleria* cf. *viridis* (dashed area). Closed and open circles indicate the species presence and absence respectively. (◄ – macrofauna sampling site; ◄ – plankton sampling site).

2.2. Sampling and Processing of Samples

The sampling sites where plankton and benthic stages of *Marenzelleria* cf. *viridis* were collected were selected according to several characteristics: located in transition between sea and estuary and experience common sea and freshwater mixing events; according to earlier studies they are typical sites in respect to the structure of bottom and plankton communities, and within an easy reach as well as suitable to use hand operated tube corer (for sampling of benthic worms) and plankton net (for sampling of pelagic larvae).

All benthic samples were taken at a permanent site (Fig. 1) in depths between 0.7 to 1.0 m using hand operated corer (diameter 10 cm, penetration depth down to 40 cm). Between 10 and 30 samples

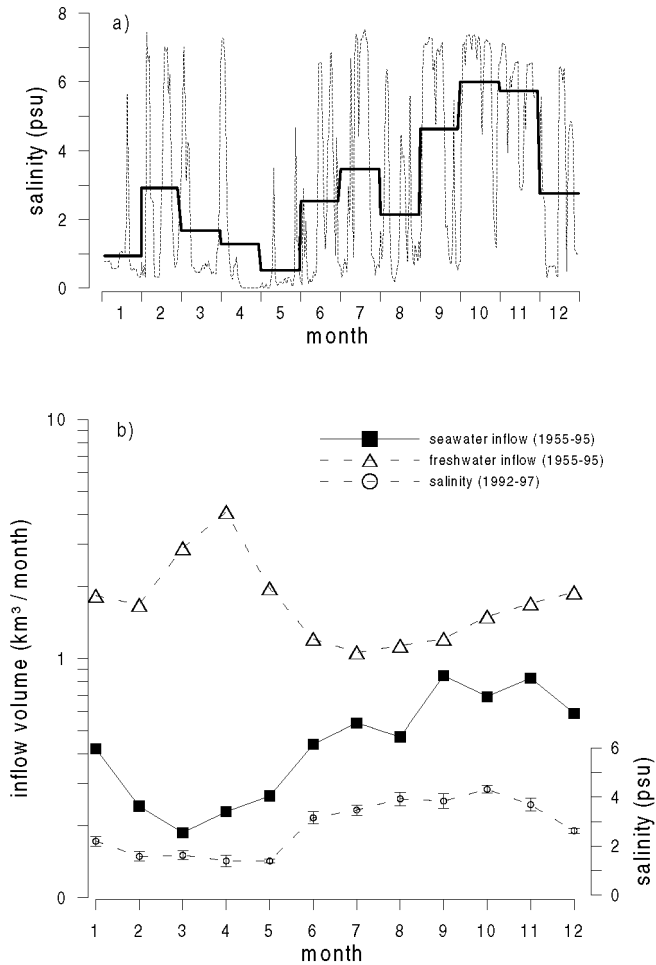


Figure 2. a) Daily salinity changes and monthly average values measured close to the plankton sampling site in the Curonian lagoon during study year (not published monitoring data from Marine Research Centre, Klaipeda); b) sea- and freshwater inflow dynamics (long-term data from GAILIUSIS *et al.*, (1996) versus average salinity (calculated from daily values, monitoring data from Marine Research Centre) in the Curonian lagoon.

were collected once or twice a month from May to December 1996. Samples were sieved using 500 μm mesh size until August and 250 μm during subsequent months, when first pelagic larvae of *M. cf. viridis* usually appear in the plankton (BOCHERT *et al.*, 1996a). The residue was transported to the laboratory in biotope water and specimens of *M. cf. viridis* were immediately sorted out. Morphometric measurements were carried out after anaesthesia in MgCl_2 10% solution for 20 min. Analysis of size structure was based on the width of 10th segment measured under microscope to the nearest 0.1 mm. Additionally, the number of segments, body length and wet weight were determined for all individuals found. Three cross-lateral sections on the reproductive part (from the 50th segment to the end of the posterior part) of the worms were produced after further fixation in 4% neutralised formaldehyde solution. The largest diameters of 20 randomly selected eggs were measured under a microscope at $\times 64$ magnification.

Between 2 and 5 worms were taken monthly from June 1996 to March 1997 (except August and February) for determination of glycogen content in the tissues as an indicator of energy budget. Measurement of glycogen was performed according to SCHÖTTLER *et al.* (1990).

All plankton samples were taken at a site in the lagoon-sea transition area (Fig. 1) approximately 7 km downward the site of the permanent benthic population sampling. During July–December samples were collected every three-four days, whereas during the rest of the study period plankton was sampled once or twice within two weeks. One vertical haul was taken during each sampling with a plankton net of 150 μm mesh size (0.13 m diameter) from 3–4 m depth. Samples were fixed with 4% neutralised formaldehyde solution. Stages of larval development were determined from individual segment number. In every sample density of each developmental stage was determined as well as the total number of larvae.

3. Results

3.1. Late Phase of Oogenesis

Diminishing of glycogen content in the tissues of *M. cf. viridis*, indicator for energy budget, started at nearly 300 $\mu\text{mol g}^{-1}$ dry wt in June–July and continued until November reaching values of 20 $\mu\text{mol g}^{-1}$ dry wt (Fig. 3). During the same period of time the diameter of oocytes increased in the adults. In a few specimens diameter of the eggs first reached a value of 100 μm in late August and in the beginning of September, when glycogen amount was nearly 120 $\mu\text{mol g}^{-1}$ dry wt. A few weeks later about 25% of the females were ripe. During this period water temperature decreased by ten degree down to 11 °C. In mid November at a temperature of nearly 7 °C all females were found with gametes ready to spawn, however the eggs were still not released. The number of non-mature and growing

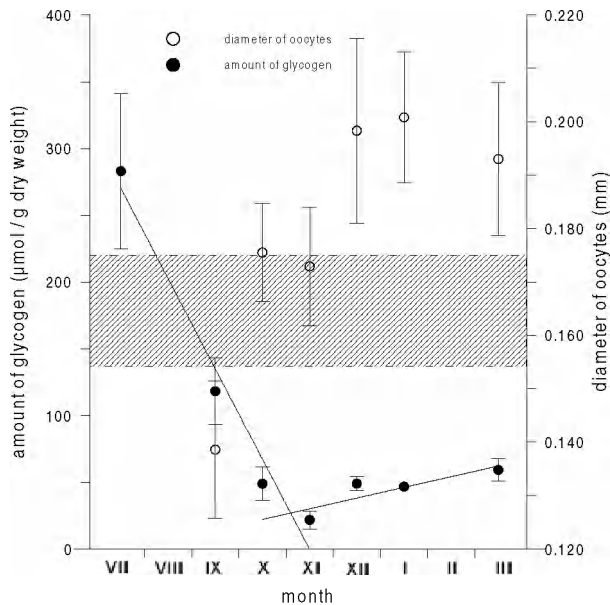


Figure 3. Glycogen amount (mean \pm SD) in μmol per g dry weight in tissues of adult worms and diameter of oocytes (mean \pm SD) during the study period. Dashed area – diameter range of mature oocytes (after BOCHERT, 1997).

oocytes was considerably low until the end of November. Though a further rise in egg diameter was delayed and the mean ($\sim 175 \pm 13 \mu\text{m}$) was similar to the value reached in October. The relationship between diameter of eggs and glycogen content became positive during November–December, when the amount of reserve material started to increase. This shift was followed by an overdraw of the upper boundary of the mature oocytes range up to an average egg diameter of $198 \mu\text{m}$. This coincided with an increased number of changed oocytes. Such changes were only detected occasionally one month before, but were typical for 30–90% of the oocytes in December. The diameter of these eggs has increased up to 50–60% of the mature size, whereas the yolk was significantly reduced. Eggs were far from discuss-shape. The typical uniform distribution of cortical alveoli imbedded the yolk around was apparently disordered. Neither clear egg structure nor alveoli around the yolk were visible in the largest oocytes. Altered oocytes were obviously denser in the posterior end of specimens.

In late January the total number of oocytes found has decreased and mean diameter in all individuals was nearly $204 \mu\text{m}$. In March a single female with remains of oosorptive eggs and still few mature oocytes were found in the samples.

3.2. Structure and Dynamics of Plankton Population

Fertilised eggs and further development stages of pelagic larvae appeared in the plankton community of the lagoon from late August. The highest densities (up to $530,000 \text{ ind}/\text{m}^3$) were found during October, when water temperature was around 10°C (Fig. 4). During November, when temperature was below 7°C , the densities were one order of magnitude lower and did not exceed $10,000 \text{ ind}/\text{m}^3$. A further decrease from about $100 \text{ ind}/\text{m}^3$ down to

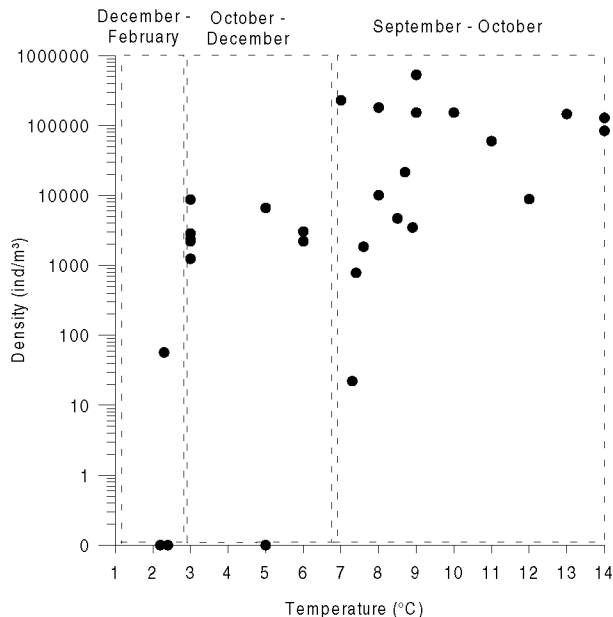


Figure 4. Density of *Marezzelleria cf. viridis* pelagic larvae vs. water temperature in the Curonian lagoon (sampling site as indicated in Fig. 1) during late reproduction period. Data from different periods separated by dashed lines (densities in freshwater excluded).

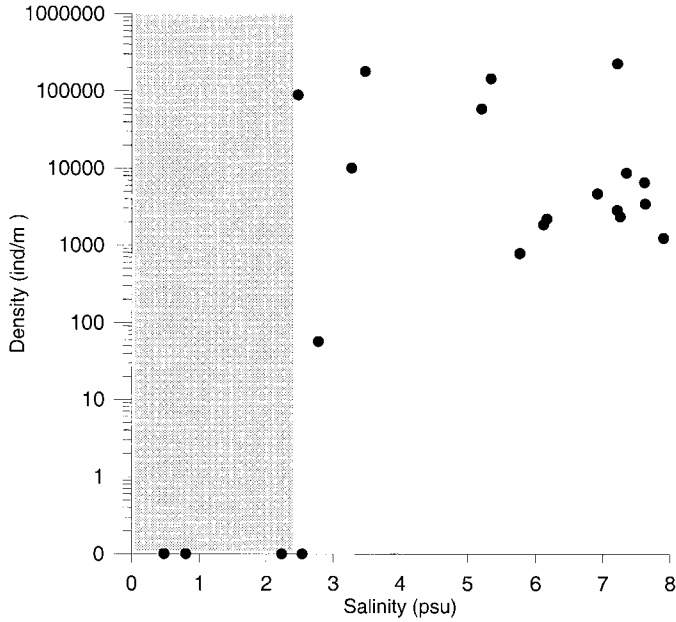


Figure 5. Density of *Marenzelleria* cf. *viridis* pelagic larvae vs. salinity in the Curonian lagoon (sampling site as indicated in Fig. 1) during late reproduction period. Dashed area indicate critical salinity range, when pelagic stages were not found.

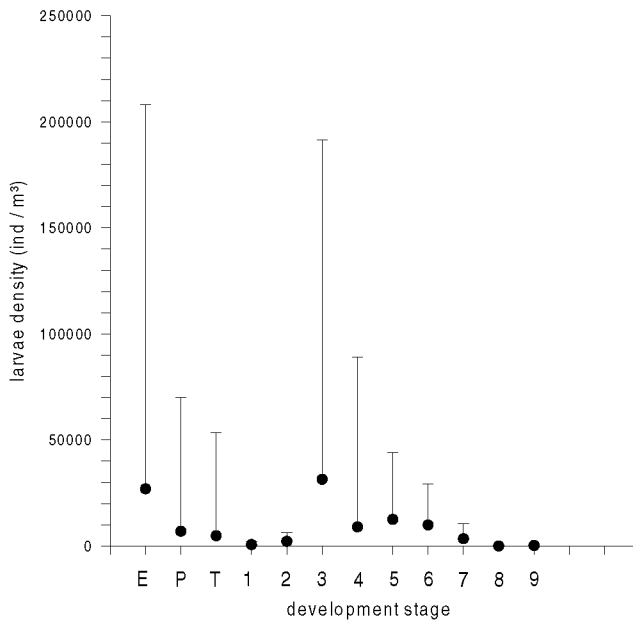


Figure 6. Mean density of different development stages of *Marenzelleria* cf. *viridis* in the Curonian lagoon during the study period (E – eggs, P – pre-trochophores; T – trochophores; numbers (0 . . . 9) indicate stage of larvae according to the number of segments). Bars – max. density reached.

complete extinction of the species pelagic stages was observed at temperatures below 3 °C. The outbursts of *M. cf. viridis* in the plankton community were related to the seawater inflows into the lagoon (Fig. 5). Generally, salinity values above 2.5 PSU indicate periods of seawater inflows into the lagoon, retention and mixing of water masses within the system as well as start of subsequent outflow. Plankton larvae were never found during established freshwater runoff, below a salinity of 2.5 PSU.

Density of *M. cf. viridis* larvae decreased even if the seawater was retained in the lagoon and salinity did not fall significantly for several days at a temperature around 3 °C. The mortality rate was estimated to be nearly 40% per day under these conditions.

The early development stages from fertilised eggs to 3-setigers were the most abundant in the *M. cf. viridis* plankton population. They accounted for more than 60% of the total larvae density. However, contribution of 3-setigers stage was essential (more than 25% of the total density) at a temperature between 8 and 10 °C. The rapid development of the eggs towards 3-setigers was characteristic according to the structure of the species plankton population (Fig. 6). Planktotrophic stages accounted only for 5 to 8 percent and they were exceptionally rare at temperatures below 4–5 °C. Only few non-fertilised eggs were found during the study period. A development boundary was found near the 10-segments stage.

3.3. Size structure of Benthic Population

At the permanent sampling site where benthic *M. cf. viridis* were collected the density of the species did not vary significantly during the study period (mean density 250 ± 70 ind/m²). Two cohorts of adults were dominant in the population (Fig. 7). One group of specimens had a body width of 1.2–1.8 mm, aging 3–7 months according to the average growth rate estimated by ZETTLER (1996). The low density of this group being nearly 30 ind/m² and less than 20% of the total benthic population indicate a poor recruitment rate during the previous reproduction season. This group appeared not to be distinguishable from the other cohort in the size frequency distribution from September onwards.

A group of few newcomers with a segment width of 0.5 mm, newly metamorphosed to benthic juveniles, was found in October. Their density did not exceed 25 ind/m² and individuals of this group contributed to less than 6% to the total abundance during the first month of their occurrence. No metamorphosed juveniles were found during the subsequent months.

4. Discussion

Two polychaete worms, *Nereis (Hediste) diversicolor* and *Marenzelleria cf. viridis*, are dominant among burrowing macrofauna species in the northern part of the Curonian lagoon (OLENIN, 1997). Since in other Baltic regions low or negligible correlations between these species were found in earlier studies on *M. cf. viridis* (ZETTLER, 1996), it was assumed that there are no important biotic interactions that limit the distribution of this spionid within the Curonian lagoon. Environmental variables associated with food supply for deposit feeders (organic content of the sediments, chlorophyll concentration, phytoplankton density) were similar to other polytrophic regions in the southern Baltic Sea, where *M. cf. viridis* successfully followed its normal life cycle (KUBE *et al.*, 1996). However, rapid water exchange between the lagoon and the sea and the following changes in salinity resulted in i) a limited development of plankton stages; ii) restriction in distribution to areas influenced by the seawater inflows, and iii) dominance of old year classes in the benthic population. Nevertheless there were certain periods only, when salinity was of importance for the local population of *M. cf. viridis*.

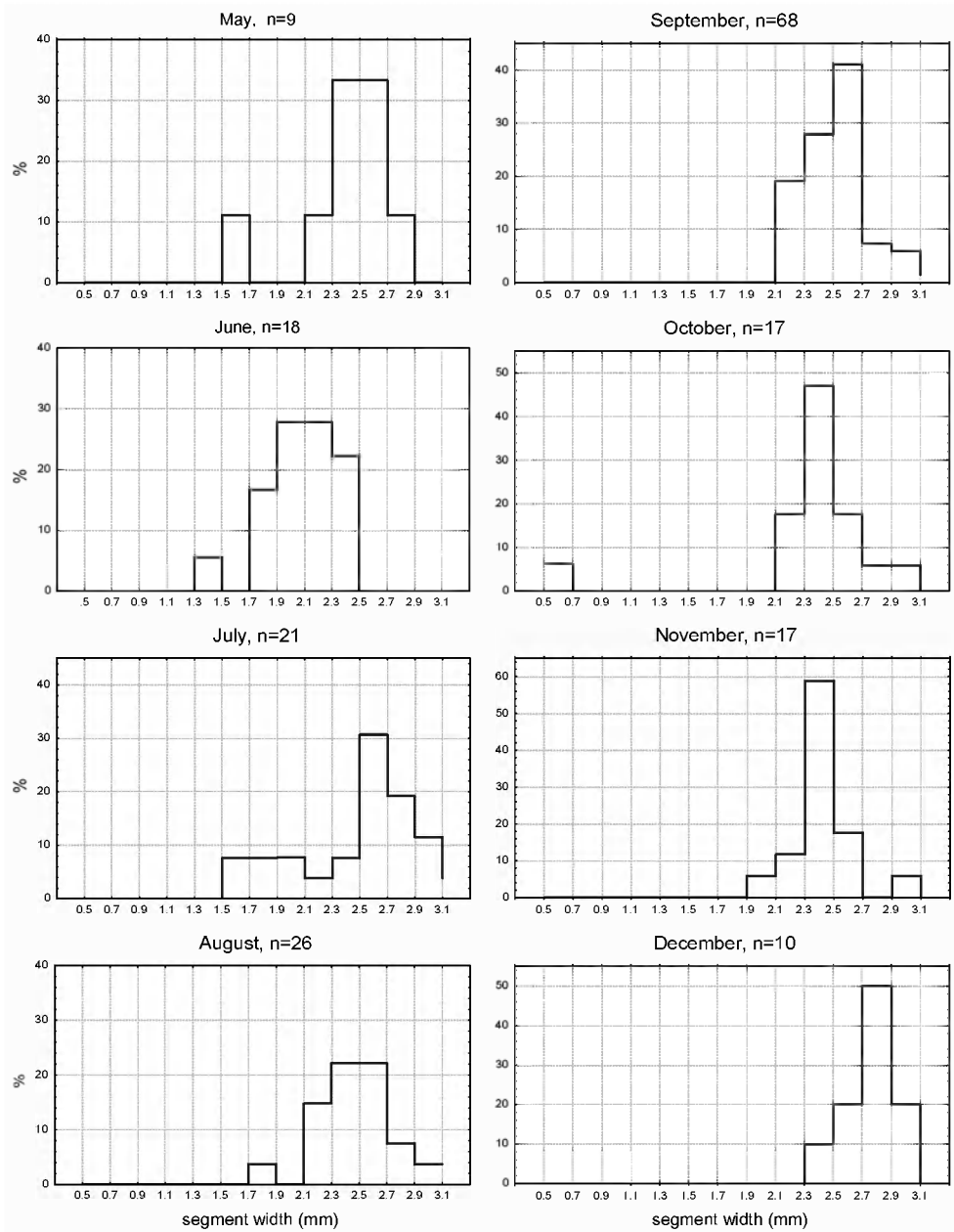


Figure 7. Size-frequency histograms of *Marenzelleria* cf. *viridis* benthic population in the Curonian lagoon during 1996 (sampling site as indicated in Fig. 1).

4.1. Life Cycle of *M. cf. viridis* in the Curonian Lagoon (South-Eastern Baltic)

In spite of almost freshwater conditions in the lagoon during vitellogenesis of *M. cf. viridis* (average 2.5 PSU) breeding was successfully completed in late October until temperature did not drop below 8 °C. This is the usual spawning time reported for this species in the south-western Baltic (BOCHERT *et al.*, 1996a). A similar independence of maturation success from ambient salinity was noticed by BOGUCKI (1963) and GASIŪNAS (1956) during field studies on the brackish polychaete *H. diversicolor*. However, in the experiment at stable salinities of 0.5 and 1.5 PSU and 20 °C *M. cf. viridis* was unable to reach maturity (BOCHERT, 1997). Our results from the Curonian lagoon document a limitation of reproduction during the final phase of egg development, visible in the delayed release of ripe gametes until November and the starting oosorption. *M. cf. viridis* did not respond to the frequent salinity rises during seawater inflows and most likely accidental salinity drops were crucial for spawning initiation. Observed spawning failure being a common phenomena of polychaetes restriction is usually induced by harsh environmental conditions and frequent in areas where a species meets its limit of range (OLIVE *et al.*, 1981; OLIVE, 1984; ECKELBARGER *et al.*, 1984). Energy which is not used during reproduction might be regained from unspawned gametes and allocated to somatic tissues (BENTLEY and PACEY, 1992). In the lagoon population of *M. cf. viridis* the delay of gametes maturation during final phase of reproduction was followed by an increase of the glycogen amount in tissues. Continuous sequence of these processes generally could be seen as a recovery of energy from unspawned gametes.

Changes in structure of the species plankton population which could be associated with spawning event in the Curonian lagoon were not observed as well. Occasional species presence in the plankton from September until mid December and its coincidence with the seawater intrusions confirm the important role of larvae drift from the sea to the lagoon plankton community. However, this way of local population maintenance resulted in a very low recruitment rate, since a development boundary at the 10-segment stage was found for the pelagic larvae. Consequently, both spawning event and development of pelagic stages were critical phases in the species life cycle in the Curonian lagoon, responding to salinity fluctuations rather than to its average.

The continuous turnover of age classes is of exceptional importance for species with relatively short life spans (*e.g. M. cf. viridis*). Few unsuccessful reproductive seasons could result in their complete extinction from the colonised habitat. However, data on bottom macrofauna show permanent presence of *M. cf. viridis* in the lagoon since its invasion (OLENIN and CHUBAROVA, 1994; DAUNYS and OLENIN, 1999; own observations). Therefore, questions concerning population maintenance should be addressed to the nearby established population.

4.2. Strategy of *M. cf. viridis* in the Stressed Habitat of the South-Eastern Baltic Sea

Recently it was concluded that the species has found its permanent niche and has become an established species of the coastal macrofauna in the Baltic Sea (ZETTLER, 1996; BOCHERT, 1997; ZMUDZINSKI *et al.*, 1997). Although a boundary at the 50 m depth was reported (ZMUDZINSKI *et al.*, 1997) in the south-eastern part of the Baltic Sea, there were no further evidences on *M. cf. viridis* limitation in the coastal zone. Our results support the hypothesis, that the *M. cf. viridis* population there is acting as a "source" of specimens, so that a considerable part of its offspring may be directed to the maintenance of local populations in stressed habitats. Rough estimates of the number of larvae transported into the Curonian lagoon show that they approximate for 0.01–0.05% of the reproductive output of the sea population, distributed close to the lagoon. Only 0.1–1.0% of those larvae that

potentially “visited” the lagoon, underwent metamorphosis to benthic juveniles there. This recruitment is negligible compared to the density of the local benthic population in the lagoon. It is more likely that migration of juveniles during post-reproductive seasons attribute to a major part to population maintenance. Migration capability of *M. cf. viridis* juveniles was reported for the Baltic (ZETTLER, 1993) and Atlantic coast of N. America (DAUER *et al.*, 1980; DAUER *et al.*, 1982). It seems that this species ability ensures permanent existence of the local population within the Curonian lagoon. The possibility of a successful reproduction of the lagoon population during some exceptional years could not be completely excluded. However, frequent fluctuations in a broad salinity range most likely fate an accidental nature of population recruitment and reproduction success in the lagoon every year. Therefore, the species establishment is supported not only by habitat suitability for juveniles and adults, but also because these stages are repeatedly reinforced from the nearby population, which breeds successfully.

5. Conclusions

The results obtained in this study indicate an extremely high tolerance of the *M. cf. viridis* adults to frequently fluctuating freshwater/oligohaline conditions unless gametogenesis is finished. Spawning event and development of pelagic larvae are critical stages in dynamic environment during the species life history. Long lived pelagic larvae, being the species advantage to disperse over extended distances does not ensure expansion even into the close distributed stressed habitats. The key force driving the species expansion into adverse environment appears to be the dispersal of relatively more tolerant benthic stages. This way of population maintenance may guarantee a permanent existence of the species over several years but with a very low density.

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