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Journal of Sea Research

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Seasonal population dynamics of the invasive polychaete genus *Marenzelleria* spp. in contrasting soft-sediment habitats



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ARTICLE INFO

Keywords: Invasion Spionid polychaete Productivity Marenzelleria viridis Marenzelleria neglecta Marenzelleria arctia

ABSTRACT

Three species of the invasive polychaete genus *Marenzelleria* are among the dominant benthic taxa in many, especially deeper, areas in the Baltic Sea. The population dynamics of the polychaetes in the Baltic are, however, still largely unknown. We conducted monthly samplings of the benthic communities and environmental parameters at five sites with differing depths and sediment characteristics in the northern Baltic Sea (59°50.896′, 23°15.092′) to study the population dynamics, productivity and growth of *Marenzelleria* spp. from April 2013 to June 2014. The species of *Marenzelleria* occurring at the study sites were identified by genetic analyses. At the deepest site (33 m) only *M. arctia* was present, while all three species were found at the shallower, muddy sites (up to 20 m depth). At the shallow (6 m) sandy site only *M. viridis* and *M. neglecta* occurred. The sites differed in the seasonal dynamics of the *Marenzelleria* spp. population, reflecting the different species identities. The muddy sites up to 20 m depth showed clear seasonal dynamics, with the population practically disappearing by winter, whereas more stable populations occurred at the deepest site and at the sandy site. The highest density, biomass and production were observed at the 20 m deep, organic-rich muddy site where all three species recruited. The seasonally very high densities are likely to have important consequences for organic matter processing, and species interactions at these sites. The observed high productivity of the populations has possibly facilitated their establishment, and considerably increased secondary production in especially the deeper areas.

1. Introduction

Communities are composed of populations of individuals of different species, and their interactions lie at the heart of ecological research. To understand single observations, we need to consider them in the context of the interacting individuals or populations for them to have any relevance. Change both in space and time is an intrinsic attribute of natural ecosystems, and a dynamic population is expressing these changes responding to changes in both the abiotic and biotic environment. Studying the populations and their dynamics will thus give us an insight into their possible interactions with their environment and is therefore essential from a conservation and management point of view (Ranasinghe et al., 2012).

Invasive species are often seen as a threat to native ecosystems due to their possible negative effects on biodiversity and ecosystem functioning (Ehrenfeld, 2010; Mack et al., 2000). Due to their demonstrated and hypothesized negative effects, a large part of research in invasion ecology focuses on how to prevent invasions or how to manage already established populations. In trying to manage invasiveness and predict

the spread of populations, as well as their interactions with the environment, knowing the species' population biology is essential. On the other hand invasions also offer a great opportunity to study basic processes in population dynamics (Sakai et al., 2001). How the system will respond to an invasion depends on the properties or traits of the introduced species as well as the properties of the system being invaded, and their interaction (e.g. Bohlen et al., 2004). Therefore it becomes increasingly important to know both your species, and your system when analyzing the effects of the invasion on for example ecosystem functioning. Studying population dynamics and factors affecting it also enables us to make predictions about the future population under changing environmental conditions.

The polychaete genus *Marenzelleria* spp. was first observed in the Southern Baltic Sea in 1985 and by 1990 it had reached the northern Baltic Sea (Bick and Burckhardt, 1989; Stigzelius et al., 1997; Norkko et al., 1993). Now the genus occurs nearly everywhere in the Baltic with a total of three species of the genus observed (Kauppi et al., 2015; Bastrop and Blank, 2006; Blank et al., 2008). *M. viridis* (Verrill, 1873) and *M. neglecta* Sikorski and Bick, 2004 are of North American origin,

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and M. arctia (Chamberlin, 1920) of European arctic origin (Blank et al., 2008). M. viridis has also been introduced to the Pacific coast of North America (e.g. Ranasinghe et al., 2012). The population and recruitment dynamics of the different species over the year are largely unknown in the Baltic Sea. Previous results on population dynamics and settling of larvae (e.g. Simm et al., 2003) have to be questioned due to the uncertainty in species identification, which is only possible by genetic analyses (e.g. Blank et al., 2008). Given that the invasive polychaete genus is one of the most dominant benthic species in many areas around the Baltic Sea (Kauppi et al., 2015), it is surprising how little we know about its basic biology and ecology. Even the occurrence and habitat preferences of the three different species are unknown in most of the Baltic Sea, Furthermore, its effects on the ecosystem functioning, for example affecting nutrient cycling through bioturbation and bioirrigation, might be substantial and vary over seasons and areas, and between the three species (Kauppi et al., 2017; Renz and Forster, 2013, 2014; Norkko et al., 2012; Hietanen et al., 2007). Additionally, few studies have during recent decades quantified seasonal changes in the macrofauna communities or their productivity in the Baltic Sea over a whole year leaving a large gap in our knowledge about the dynamics of this system over the winter, and after changes in species composition have taken place (but for some older studies see e.g. Segerstråle, 1937, 1962; Sarvala, 1971; Elmgren, 1978; Elmgren et al., 1986; Uitto and Sarvala, 1991; Lehtonen, 1996).

Our aim was to study seasonal dynamics and factors affecting the populations of *Marenzelleria* spp. in the northern Baltic Sea, and analyze the growth and productivity of *Marenzelleria* spp. populations from shallow (5 m) to deep (33 m) coastal habitats. A further aim was to identify the species present at the study sites, for which genetic material was collected. This was done in order to better understand and predict the future impacts of this species complex on the Baltic Sea ecosystem.

2. Material and methods

2.1. Sampling design

Population dynamics of *Marenzelleria* spp. were studied at five different locations in the proximity of Tvärminne Zoological Station in the southernmost Finland (59°50.896′, 23°15.092′). Site I is a muddy, unvegetated site with a depth of 5–6 m situated at the inlet into a bay. Site II is an unvegetated, muddy site at 10 m depth. Site III has a depth of 20 m and the sediment consists of a looser muddy layer on top of more dense clay. Site IV has a depth of 33 m and very loose mud bottom. Site V also has a depth of 5–6 m but in contrast to site I, this site is more exposed to winds and wave action from the open sea, and has sandy sediment.

At sites I-IV sampling was conducted monthly starting in April 2013 and ending in June 2014, with the exception of December 2013 and February and April 2014, when sampling was not conducted due to challenging winter conditions. Site V was sampled from May 2013 onwards monthly until December 2013, except in November, and again in March and June 2014. In April and May 2013 at sites I-IV, three replicate samples were taken with a Limnos sediment corer (9.3 cm in diameter) from the ice or from a small boat. From June 2013 until June 2014, three replicate samples were taken with a Gemax twin corer (9 cm in diameter) at sites I and III and five replicate samples at sites II and IV. At site V six replicate samples were taken by SCUBA diving using acrylic core liners with a diameter of 5.6 cm.

The top 1 cm of the core samples was sliced and sieved gently through a 200- μ m sieve in order to collect the newly settled larvae. The total depth of the sediment in the cores varied from 8 cm at site V (sandy sediment) to approximately 30 cm at sites I to IV, always extending below the depth of the fauna in the sediment at the site. The rest of the sample was sieved through a 500- μ m sieve. The benthic samples were fixed in 70% ethanol and dyed with rose Bengal and sorted later under microscope. Biomasses are reported as g wet weight

 ${\rm m}^{-2}$ of blotted individuals, which means that the biomass of newly settled specimens is not included due to their small size.

2.2. Environmental factors affecting densities and biomasses at the different sites

In addition to benthic core samples, a number of environmental parameters were measured on each sampling occasion. Data from the near-bottom water (< 1 m) for temperature and salinity were obtained with a CTD device and oxygen (mg L⁻¹ and %) was measured with an YSI proODO oxygen meter. Sediment organic content (measured as loss on ignition, LOI). C/N ratio and grain size were determined from the top cm of sediment from an additional core taken at each site at each time. For determination of the organic content, the sediment was first dried at 60 °C for 48 h and thereafter burned at 500 °C for 3 h and the organic content was calculated from the difference in weight of the samples. For C/N, approximately 30 mg (sandy sediment) or 10 mg (muddy sediment) of dried (60 °C for 48 h), acidified sediment was analyzed for carbon and nitrogen content. Grain size distribution was determined by sieving the sediment sample through a series of sieves (2, 1, 0.5, 0.25, 0.125 and 0.063 mm) after which the sediment retained in the sieves or in the pan was dried (60 °C for 48 h) and weighed.

Pearson product moment correlations were calculated between environmental factors (temperature, salinity and dissolved oxygen (DO) in the bottom water, sediment organic content (OM) and C/N) and the average density of *Marenzelleria* spp. per sampling (an average of 3 to 6 replicates per sampling, depending on the site) to investigate relationships between the seasonal variation in the environment and the density of the *Marenzellleria* spp. population. Due to autocorrelation in the time series, correlations were also calculated between the density at t $+\ 1$ and the environmental predictors at time t.

2.3. Population dynamics, growth and production

The maximum width of *Marenzelleria* spp. at the widest part of the worm (usually near the 10th segment) was measured with an ocular micrometer and used as an estimate of size to identify cohorts and to measure growth. Biomass of all species was measured as wet weight of blotted animals. For growth measurements of *Marenzelleria* spp., selected individuals from representative size classes were remeasured and dried for 48 h at 60 °C and weighed. The dry weight was regressed against the width of the worm and the regression was then used to convert the width of all specimens to biomass.

Different cohorts were identified to estimate recruitment, longevity and growth of the individual in the population following the method of Bhattacharya (1967) (TropFishR -package, Mildenberger and Taylor, 2017). Secondary production and production to biomass -ratios (P/B -ratio) for each cohort were calculated following Brey (2001). The Increment Summation Method (ISM) was used to assess the production and P/B -ratios for the whole population (Brey, 2001).

2.3.1. Individual growth rates and factors affecting growth

Individual growth rates were modeled using the von Bertalanffy growth equation (Brey, 2001). Both the specialized and generalized von Bertalanffy growth models were tested. Generalized von Bertalanffy growth model had the best fit for all cases:

$$S_t = S_{\infty}{}^* (1 - e^{-K^*(t-t0)})^D$$

where S_t is size at time t, S_{∞} is the infinite size of the species, K is the growth constant defining how fast the asymptote is reached, and D is the shape parameter determining the shape of the curve, which is more or less sigmoid.

The growth parameters were defined separately for all the sites. At site IV with the confirmed occurrence of only one species, and at site V with the confirmed occurrence of two species, the growth parameters were also iterated separately for the distinguishable cohorts during the

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