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Benthic competition and population dynamics of *Monoporeia affinis* and *Marenzelleria* sp. in the northern Baltic Sea

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ABSTRACT

During the last two decades major changes of the benthic fauna have occurred in the northern Baltic Sea, the Gulf of Bothnia. The native amphipod, *Monoporeia affinis*, has shown a large-scale abundance decrease, while polychaetes, *Marenzelleria* spp. have invaded the system. *Marenzelleria* co-exist with the native fauna in the southern Baltic Sea, but in the north the pelagic production might be too low to allow co-existence. Thus, *M. affinis* might have been out-competed by *Marenzelleria* in the Gulf of Bothnia. This hypothesis was tested in a competition experiment with a high and a low fresh phytoplankton food supply. When exposed to high food supply both species showed stable or increased biomass over the four week test period. In low food supply, however, *M. affinis* was found to have a competitive advantage. The experimental data were also related to Baltic Sea monitoring data on primary production, sedimentation and invertebrate abundances. Data from the northern Baltic Sea show that the dominance in the benthic community by *M. affinis* was replaced by *Marenzelleria* around 2001. The amphipod decrease might be explained by a marked decrease in primary production during this period. Combining monitoring and experimental data suggests that the invasion of *Marenzelleria* did not cause the decrease of *M. affinis* in the northern Baltic Sea; it rather took advantage of the density gap that had occurred. A shift may thus have been established in the Bothnian Sea benthic community.

1. Introduction

In brackish water systems, species diversity of organisms is generally low and the food webs are built up by relatively few native keystone species (Remane, 1934, 1971; Bonsdorff and Pearson, 1999). This condition of an ecosystem has been suggested to make it extra vulnerable to disturbances, by relatively easily altering the structure, function and stability of the food web (Cardinale et al., 2006; Duffy et al., 2007). The Baltic Sea is a rather young brackish water ecosystem, heavily affected by anthropogenic disturbances of both abiotic and biotic characters. Introduction of non-indigenous species is one such disturbance and during the last decades more than 100 new species have been recorded in the Baltic Sea (Olenin and Leppäkoski, 1999). About 70 of these introductions have established reproducing populations (Leppäkoski et al., 2002), and the high success rate might be explained by the relatively low species diversity, as low diversity systems have less invasion resistance (Stachowicz et al., 1999).

Invasive species are often suggested to have unique traits that give them competitive superiority compared to native species (Byers, 2000). In the past, focus has been on negative consequences of invaders, such as extinction of native species, but in recent years it has become evident that the situation is more complex, demonstrating influence on the fundamental structure and function of an ecosystem by new species affecting the biogeochemical pools and fluxes of materials and energy (Ehrenfeld, 2010). The polychaete *Marenzelleria* is an example of a successful invader in the Baltic Sea affecting sediment chemistry by increasing oxygenation and nutrient fluxes (Karlsson et al., 2011; Norkko et al., 2011). In the southern Baltic Sea, it was observed as early as 1985 (Schiedek, 1997), but not until 15 years later this species invaded the Gulf of Bothnia. During the corresponding period one of the native key benthic species, the deposit feeding amphipod *Monoporeia affinis* (Lindström) (Amphipoda: Crustacea), showed a large-scale decline, which might suggest that the *Monoporeia* suffered from competition from *Marenzelleria* (Kotta and Ólafsson, 2003). Experiments have shown that moderate polychaete densities affect the amphipod sediment-preference and growth negatively (Kotta and Ólafsson, 2003; Neideman et al., 2003). Other possible causes

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for the *Monoporeia* decrease may have been e.g. strong predation from the benthic isopod crustacean *Saduria entomon* (Englund et al., 2008) or a combination of high amphipod densities and severe food limitation due to a decrease in phytoplankton primary production (Eriksson Wiklund et al., 2008, 2009).

Soft-bottom sediments depend on the supply of organic matter from settling phytoplankton blooms (Graf, 1992). In the Baltic Sea, the primary production is 10-fold higher in the southerly Baltic Proper than in the northerly Bothnian Bay, whereas the bacterial production is relatively similar in the different basins (Samuelsson et al., 2006). During the period 1998–2001 the amphipod population decrease coincided with higher precipitation than normal causing an increased river run-off of terrestrial dissolved organic material to the Baltic Sea (Wikner and Andersson, 2012). This induced a structural change in the pelagic food web, amplifying the importance of the heterotrophic microbial food web over the herbivorous food web, which has phytoplankton as the base (Berglund et al., 2007). Such a change in the pelagic food web would reduce benthic productivity, since microheterotrophs have lower settling rates than phytoplankton. The effect of such shifts on benthic production was examined by Eriksson Wiklund et al. (2009), showing that the growth *Monoporeia affinis* was severely affected by a shift from a phytoplankton-based towards a bacteria-based pelagic production.

The concomitant decrease of *Monoporeia* and phytoplankton primary production and increase of *Marenzelleria* in the Gulf of Bothnia during the period 1998–2001 (Wikner and Andersson, 2012), suggest that *Monoporeia* might be a poor competitor for resources at low food availability. The resource availability might have reached a threshold where *Monoporeia* no longer was competitive and *Marenzelleria* therefore could increase its importance in the benthic community. Such a population decrease of *Monoporeia* did not occur in the Baltic proper when *Marenzelleria* invaded the system, may be because in that region the phytoplankton primary production was 10 fold higher, providing food enough for the co-existence of both benthic species. Another basis for this hypothesis is that *Marenzelleria* has lower lipid demand compared to *Monoporeia affinis*. The lipid content in *M. affinis* is as high as 20–40% (Lehtonen, 1994) and it needs a lipid content of >20% in order to reproduce (Hill et al., 1992), whereas in polychaetes the lipid content is approximately 10% (Dall et al., 1991; Magnusson et al., 2006). This further indicates that *Marenzelleria* may have a capability to outcompete *M. affinis* in the low productive Gulf of Bothnia, while this is not likely in the more productive Baltic Proper. To test if *Marenzelleria* out-competes *M. affinis* at low food availability, a competition experiment was performed between *M. affinis* and *Marenzelleria* with a high and a low pelagic food supply. The amount of phytoplankton provided as food supply to the benthic animals was dimensioned in relation to the variation of primary production and sedimentation rates in different areas of the Baltic Sea (Samuelsson et al., 2006; Gustafsson et al., 2013). The experimental results were also related to long term monitoring data from both the Baltic proper and Bothnian Sea on primary production, sedimentation, and invertebrate abundances. This study contributes to the understanding of the competitive advantages of native and invasive species in brackish water systems and to potential effects of environmental change on the benthic fauna in the sea.

2. Material and methods

2.1. Collection of benthic animals

Both species were collected by a benthic dredge the 16 and 17 of May in the Gulf of Bothnia (63° 30.5′ N; 19° 48.0′ E). The sediment was carefully sieved through a 1 mm mesh to collect the organisms. Previous studies have shown that there are three *Marenzelleria* species with more or less distinct distribution pattern that have been introduced into in the Baltic Sea: *Marenzelleria viridis* (Verril), *Marenzelleria neglecta* (Sikorski and Bick nov) and *Marenzelleria arctica* (Chamberlin) (Sikorski and Bick, 2004; Bastrop and Blank, 2006). This taxon will henceforth be referred to as *Marenzelleria*. *Marenzelleria* spp. was sorted according to size (individuals of approximately 20 ± 2 mm length were selected). *Marenzelleria* spp. was not determined to species since species determination can only be made by molecular methods (Blank et al., 2008). However, according to Blank et al. (2008), the samples are likely to be dominated by *M. arctica*, which was the only species of *Marenzelleria* found in this part of the Bothnian Sea. *Monoporeia affinis* was sorted into specific year classes, and the generation 1+ was used in the experiment (≈2 mg dry weight ind^{-1} at the start of the experiment). The sorted organisms were then stored in brackish water for a maximum period of 48 h at 4 °C until the start of the experiment.

2.2. Phytoplankton culture

A phytoplankton culture was used as food source for the benthic organisms. The 20 l culture was based on pre-filtered seawater (100 μm) from the Gulf of Bothnia, which was enriched every third day with 158 μM nitrate, 26 μM ammonium and 12 μM phosphate, respectively. The phytoplankton culture was maintained in a slow flow through system, exchanging 2 l of water every day. Light was set to 100 μmol quanta m^{-2} s^{-1} for 12 h per day. Oxygen was mixed into the culture through air stones. The phytoplankton concentration was checked prior to addition by measuring the chlorophyll-*a* concentration. 50–100 ml water was filtered through GF/F filters and extracted in 95% ethanol for ~2 h in the dark. Approximately 90% of the Chl *a* was found to be extracted by using this relatively short extraction time. Samples were analysed in a Perkin Elmer LS30 fluorometer (433 nm excitation wavelength and 674 nm emission wavelength). Phytoplankton carbon biomass was estimated using a conversion factor of 50 μg C/μg Chl *a*, which should be accurate for the spring period (Andersson and Rudehäll, 1993). To monitor which phytoplankton groups were used as food source for the benthic organisms, 50 ml samples were fixed with 150 μl Lugols solution and analysed using the Uthermöhl technique. 2–8 ml samples were settled overnight in Hydrobios chambers and analysed in an inverted microscope (Nikon) at 200 times magnification. Carbon biomass concentrations of different taxonomic

Table 1
Experimental design. Densities of *M. affinis* and *Marenzelleria* sp. in aquaria with high and low food availability and with and without competition. The 6 different treatments were replicated 4 times.

Food addition	Phytoplankton (mg C m^{-2} day^{-1})	Competition *M. affinis* and *Marenzelleria* sp. (Individuals m^{-2})	No competition *M. affinis* (Individuals m^{-2})	No competition *Marenzelleria* sp. (Individuals m^{-2})
High	18.4	1984 and 992	1984	992
Low	0.3	1984 and 992	1984	992