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Changes in the feeding behaviour of benthic invertebrates: effect of the introduced polychaete *Marenzelleria viridis* on the Baltic clam *Macoma balthica*

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Abstract. The exploited feeding areas of *Macoma balthica* and *Marenzelleria viridis* were experimentally quantified in laboratory conditions. Our feeding trials showed that *M. balthica* was able to feed at a much wider surface area than *M. viridis*. Moreover, in the presence of *M. viridis* the feeding area of *M. balthica* and its cumulative increase in time were significantly higher than without the polychaete. These results suggest that *M. balthica* is superior to *M. viridis* in terms of feeding. The experiment supports the earlier findings that the presence of *M. balthica* appears to be a key factor limiting the further expansion of *M. viridis* in the northern Baltic Sea.

Key words: Baltic Sea, interspecific competition, invasion, *Marenzelleria viridis*, *Macoma balthica*.

INTRODUCTION

The North American detritus feeding polychaete *Marenzelleria viridis* (Verrill) was first found in the Baltic Sea in 1985 (Bick & Burckhardt, 1989). To date *M. viridis* is practically established in the whole Baltic Sea and has become an important component of the macrozoobenthic communities (Olenin & Leppäkoski, 1999; Kotta, 2000; Leppäkoski & Olenin, 2001; Zettler et al., 2002).

The abundances of *M. viridis* in the northern Baltic Sea are however rather low, seldom surpassing 100 ind m^{-2} (Stigzelius et al., 1997; Kotta, 2000). High species diversity, increased food availability, low salinity, and uniformity of bio-

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tope facilitated the invasion of *M. viridis* in the northern Baltic Sea (Kotta, 2000; Kotta & Orav, 2001; Zettler et al., 2002).

M. viridis is ranked among the most influential exotics in the region. The species is the only deep sediment burrower deposit-feeder in the northern Baltic Sea. An addition of a novel function has the potential to cause great ecological impacts (Simberloff, 1991; Ruesink et al., 1995). Due to the active bioturbation *M. viridis* most probably improves the oxygen regime in the sediment. Besides, the addition of an efficient deposit feeder into the benthic system is likely to offset a stress on the native fauna due to possible competitive interactions for food and/or for space.

There exists circumstantial evidence that after the invasion of *M. viridis* the densities of the shallow water amphipod *Corophium volutator* (Pallas) (Atkins et al., 1987; Zettler, 1996), the polychaete *Hediste diversicolor* (O. F. Müller) (Atkins et al., 1987; Essink & Kleef, 1993; Kotta & Kotta, 1998), and the deep-water amphipod *Monoporeia affinis* Lindström have dropped considerably (Cederwall et al., 1999). Experimental studies have demonstrated the negative effect of the polychaete on *H. diversicolor* and *M. affinis* (Kotta et al., 2001; Kotta & Ólafsson, 2003; Neideman et al., 2003). However, the same experiments (Kotta et al., 2001) suggested that the dispersal of *M. viridis* in the northern Baltic Sea is probably not so successful in communities that are strongly dominated by the bivalve *Macoma balthica* L.

In this study we compared the feeding of *M. viridis* and *M. balthica* in terms of exploited feeding area. The experiment involved treatments of a single species and the combination of the two species. Our hypothesis is that the superiority of *M. balthica* over *M. viridis* is likely to be gained by higher and more efficient feeding activity of the bivalve. That is (1) *M. balthica* should feed on a larger surface area than *M. viridis* and (2) the presence of *M. viridis* should induce higher feeding activity of *M. balthica*.

MATERIAL AND METHODS

An *in situ* experiment quantifying the feeding areas of the clam *M. balthica* and the polychaete *M. viridis* was carried out in the laboratory of the Tvärminne Zoological Station in the northeastern Baltic Sea in June 2000. Altogether 15 mesocosms of 1.5 L were used to permit 3 treatments replicated 5 times. We deployed the test animals both separately and together. The test organisms were added in accordance with their abundance values in the field. The density of *M. balthica* and *M. viridis* was 350 and 175 ind m^{-2}, respectively. The average length of the test animals was 13.3 ± 0.1 and 44.3 ± 2.5 mm ($\pm$SE), respectively.

In the experiment natural sedimented phytoplankton were added to the mesocosms every 48 hours, i.e. altogether three times. The surface area of invertebrate trails on sediment surface was regularly quantified by the aid of a digital camera (Fig. 1). Prior to each feeding trial the sediment surface was

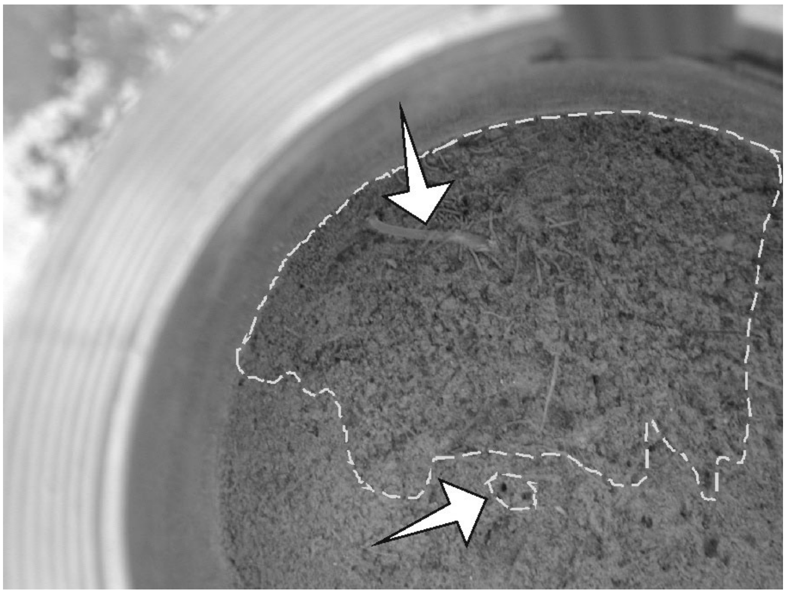

Fig. 1. A photograph of the feeding activity of the test animals: in the centre above the siphon of *Macoma balthica* and below two holes of the burrows of *Marenzelleria viridis*. Dashed lines indicate the feeding areas of both species.

carefully smoothen. The experiment lasted 5 days. We compared the cumulative increase in feeding areas between the studied species and the role of co-occurring species in affecting these functional responses. We employed polynomial linear regression analyses to describe the functional responses. The differences in the feeding areas between *M. viridis* and *M. balthica* were analysed by one-way ANOVA (Sokal & Rohlf, 1981).

RESULTS

Our feeding trials indicated that *M. balthica* was able to consume detritus at a much wider surface area than *M. viridis* (Fig. 2; one-way ANOVA, all data of single species treatments included, $p < 0.001$). Moreover, in the presence of *M. viridis M. balthica* searched more actively for food than without the polychaete (one-way ANOVA, $p = 0.003$). *M. balthica* exploited the whole surface area already in the first 5 h of the incubation whereas the feeding area of *M. viridis* did not change in the course of the experiment. *M. viridis* was highly sedentary and fed only within a few millimetre distance from its burrow. The presence of *M. balthica* had no effect on the feeding area of the polychaete (one-way ANOVA, $p = 0.152$).

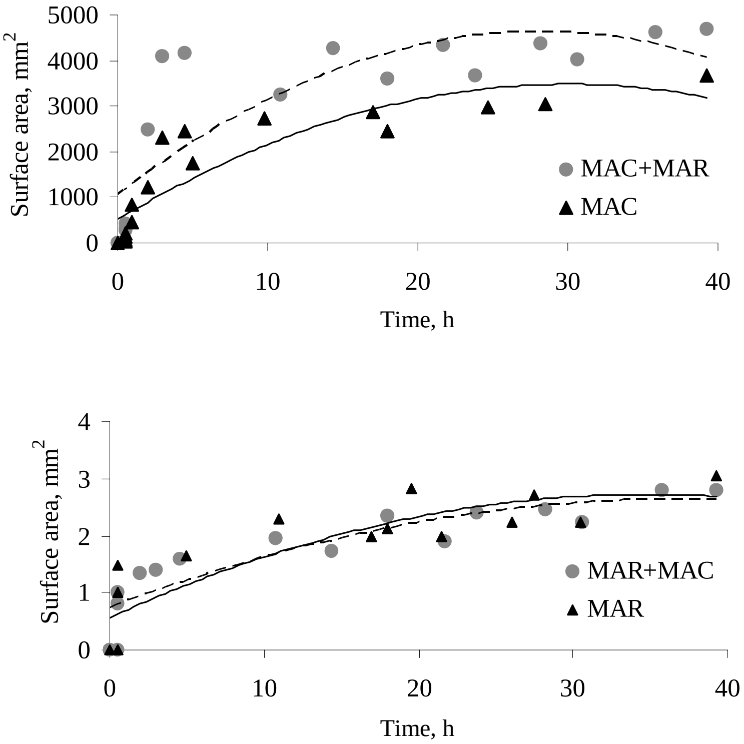

Fig. 2. Cumulative increase in the feeding area of *Macoma balthica* (MAC) and *Marenzelleria viridis* (MAR). The test animals were deployed both separately and together. The continuous line represents single species treatments and broken line the treatments where the two species were deployed together.

DISCUSSION

The polychaete *M. viridis* is primarily a subsurface deposit feeder and lives in sediment tubes. The feeding radius of the species is small unless the animal extends its body outside of the burrow. Occasionally, the polychaete may emerge from the tube in order to feed on sediment surface or perform suspension feeding (Zettler et al., 1994; Dauer, 1997; Bock & Müller, 1999). The bivalve *M. balthica* is primarily a surface deposit feeder but may also graze pelagic microalgae by suspension feeding (Hummel, 1985; Ólafsson, 1986). The bivalve lives in the upper layers of sediment and sucks food by rotating movements of the tip of the siphon. New material is ingested by moving the siphon to a new position. Thus, due to similarities in feeding mode and habitat selection the two species may compete for both food and space.

The results of our trials agreed to the hypothesis that *M. balthica* is able to search for detritus at a higher rate and at a much wider surface area than *M. viridis*. *M. balthica* searched more actively for food in the presence of

M. viridis, i.e. in the case of higher food limitation. The outcome of the experiment explains the earlier findings of the reduced survival of *M. viridis* in the presence of *M. balthica* (Kotta et al., 2001). Quick and efficient consumption of food resources typifies the opportunistic species and is beneficial in the areas where the amount of food varies highly. The prevalence of *M. balthica* in a temporally and spatially varying ecosystem such as the Baltic Sea is likely to be gained by the variety of efficient feeding modes and better tolerance of food shortages (e.g. Brafield & Newell, 1961; Ólafsson, 1986).

Besides food competition our results do not exclude physical interference as the likely explanation for the outcome of the feeding trials. Although in some mesocosms the study animals were spatially separated the bivalves responded to the presence of the polychaete. The possible mechanism behind it may be that the bivalves sense and react chemical and/or tactile signals from the worms (e.g. McClintock & Baker, 1997).

As *M. balthica* dominates on the soft bottom biotopes of the Baltic (Segerstråle, 1957; Hällfors et al., 1981) *M. viridis* should prevail only at the biotopes where the polychaete can avoid the bivalve. These are for example the sea areas adjacent to river mouths where the food for deposit feeders is in excess and the population of the bivalve is more stressed owing to low salinity. Consequently, the negative interactions between *M. viridis* and the resident fauna are less intense and the dominance of *M. viridis* is very likely in the areas (Kotta, 2000).

M. balthica is also missing in the deeper hypoxic water (Laine, 2003). This may explain the establishment success of the polychaete in the deeper waters of the northern Baltic Sea (Kotta, 2000). The ability of *M. viridis* to perform diel vertical migration (Dauer et al., 1981; Russel, 1995) is beneficial for the populations inhabiting deeper sites in order to survive the temporary anoxia that is a common phenomenon of the northern Baltic Sea. This is also in accordance with the invasion theory stating that invaders into natural aquatic systems are most likely to become established when native assemblages of organisms have been temporarily disrupted or depleted (Moyle & Light, 1996).

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Muutused põhjaloomastiku toitumiskäitumises – introdutseeritud hulkharjasussi *Marenzelleria viridis* mõju karbile *Macoma balthica*

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Laborikatsete käigus uuriti suurselgrootute toitumiskäitumist. *M. balthica* toitub palju laiemal alal kui *M. viridis*. *M. viridis*’e esinemisel suurenevad *M. balthica* toitumisala ja toiduotsingu aktiivsus oluliselt. Tulemused viitavad sellele, et *M. balthica* konkurentsieelis hulkharjasussi *M. viridis* ees on tingitud karbi efektiivsemast toitumisstrateegiast. Konkurentsisuhteid nende kahe liigi vahel võib pidada peamiseks faktoriks, mis piirab hulkharjasussi *M. viridis* edasist levikut Läänemeres.