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Competition for food between the introduced polychaete *Marenzelleria viridis* (Verrill) and the native amphipod *Monoporeia affinis* Lindström in the Baltic Sea

Jonne Kotta^{a,*}, Emil Ólafsson^b

^aEstonian Marine Institute, University of Tartu, Marja 4d, 10617 Tallinn, Estonia

^bDepartment of Zoology, Stockholm University, SE-10691 Stockholm, Sweden

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Abstract

Since 1985 the spionid polychaete *Marenzelleria viridis* (Verrill) has invaded large parts of the Baltic Sea. In deeper soft-bottom habitats (>10 m) a marked long-term decrease of the native amphipod *Monoporeia affinis* has been noted and is presently associated with the establishment of the polychaete. One plausible explanation is that the polychaetes and the amphipods are competing for food resources as both are deposit feeding animals and likely to share similar food resources. Interspecific competition for food between the polychaete and the amphipod was studied in a laboratory experiment. Two year classes (0y+, 1y+) of the amphipods were kept at various densities, with and without added food resources, with and without the polychaete, in microcosms with sediment and continuous supply of cooled water for 2 months. The polychaetes did not have any effect on mortality in the amphipods. 4-way ANOVA showed that food addition, density of amphipods and presence of the polychaete had a significant effect on the growth of amphipods of different age classes. 1y+ amphipods showed increased growth with added food and this increase was density-dependent in the absence of the polychaetes but not in their presence. The polychaetes reduced the growth of 1y+ amphipods at natural densities (2000 ind m⁻²) by 60%, but had no clear effects on the growth of juveniles. It is concluded that lower amphipod growth in the presence of *M. viridis* was caused by competition for food and is likely to affect the population of *M. affinis* in deep soft-bottom habitats of the northern Baltic Sea.

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1. Introduction

The Baltic Sea is one of the world's largest brackish water bodies. Owing to low salinity, short developing time and isolation, only a limited number of species

have been able to adapt to the local conditions (Segerstråle, 1957). Soft-bottom assemblages below the thermocline (>20 m) show particularly low species richness. For example, in the Baltic proper there are only a few species of macrofauna and about 40 to 50 meiofauna species (Segerstråle, 1957; Elmgren, 1978, 1984; Aarnio et al., 1991; Ólafsson and Elmgren, 1997).

* Corresponding author.

E-mail address: jonne@sea.ee (J. Kotta).

The amphipod *Monoporeia affinis* is found in soft sediments below 10 m practically all over the Baltic Sea. It shares its habitat with relatively few other macrofauna species and is ranked among the most abundant members in this biotope. During spring and summer the densities of *M. affinis* are normally 1000 to 2000 adults m^{-2} in the northern Baltic proper (Cederwall, 1977; Laine et al., 1997). In March–April, when juveniles (0y+) are released from the marsupium, the natural abundance may exceed 15 000 ind m^{-2} (Järvekülg, 1973; Sarvala and Uitto, 1991). The amphipods may affect the structure of benthic assemblages through high consumption of sedimented phytoplankton (e.g. Lehtonen and Andersin, 1998) and bioturbation (e.g. Ólafsson and Elmgren, 1991). They are important in the Baltic Sea food web, being efficient consumers of settling spring bloom phytodetritus (Lopez and Elmgren, 1989; Van de Bund et al., 2001) and being preyed upon by a number of demersal fish and benthic invertebrate species (e.g. Segerstråle, 1937; Leonardsson, 1991; Hill and Elmgren, 1992; Arrhenius and Hansson, 1993; Hüsey et al., 1997).

It is likely that intraspecific competition occurs in *M. affinis* populations in the Baltic Sea. Juveniles and adults share the same food resources and the same habitat. Fluctuations in the numbers of *M. affinis* correlate with primary production values (Elmgren, 1978; Uitto and Sarvala, 1990; Sarvala and Uitto, 1991) and the growth of amphipods seems to be density-dependent (Sarvala, 1986; Leonardsson, 1994). In addition to these observations, there is experimental evidence that there is competition for food within and between year classes of *M. affinis* (Hill, 1992; Elmgren et al., 2001; Wenngren and Ólafsson, 2002).

Biological invasions are known to cause large-scale ecological changes and economic damage world wide. The examples of invasions in the 1980s and 1990s have shown that successful exotics may render previously stable systems unbalanced and unpredictable (Leppäkoski, 1991; Carlton and Geller, 1993; Mills et al., 1993; Carlton, 1996; Ruiz et al., 1999) and may severely affect biological diversity in the area (Baker and Stebbins, 1965; Gollasch and Leppäkoski, 1999; Gollasch et al., 1999; Levine and D'Antonio, 1999). A number of benthic animals presently living in the Baltic have only recently invaded the area, some only in the

last decades or years (Gruszka, 1999; Olenin and Leppäkoski, 1999).

Since 1985 the North-American detritus feeding polychaete *Marenzelleria viridis* (Verrill) has invaded large parts of the Baltic Sea (e.g. Essink and Kleef, 1993; Stigzelius et al., 1997; Olenin and Leppäkoski, 1999; Kotta and Orav, 2001). The appearance of *Marenzelleria* in the North Sea and the Baltic Sea is considered to represent independent introductions (Essink, 1999). The Baltic *M. cf. viridis* is distinguished from the North Sea populations of *M. cf. wireni* on the basis of morphological, reproductional and genetical differences (Bastrop et al., 1997; Bick and Zettler, 1997; Bocher, 1997).

In several shallow soft-bottom biotopes in the Baltic, *M. viridis* has become a dominant macrofauna species at densities up to 270 000 ind m^{-2} . In general, the density of the polychaete decreases with increasing latitude (Zettler et al., 1995; Zettler, 1997). In the soft sediments below 10 m, however, the polychaetes are encountered in low but stable numbers, i.e. <200 ind m^{-2} (Kube et al., 1996; Stigzelius et al., 1997; Ojaveer et al., 1999; Kotta, 2000), but may reach 2000 ind m^{-2} in areas of organic enrichment (Cederwall et al., 1999).

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 *Nereis diversicolor* (O. F. Müller) (Atkins et al., 1987; Essink and Kleef, 1993) and the deep-water amphipod *M. affinis* have dropped considerably (Cederwall et al., 1999). In an in situ experimental study, Kotta et al. (2001) demonstrated higher mortality of *N. diversicolor* in the presence of *M. viridis* than in its absence. One plausible explanation is that the polychaetes and the native fauna are competing for food resources as both species are deposit feeding animals and therefore may share the same food resources. On the other hand, the decline of native fauna (*M. affinis*) in the Gulf of Finland has not been fully synchronised with the introduction of *M. viridis* (Kangas et al., 2001; A. Laine, pers. comm., 2002).

In this paper we investigate whether the introduced polychaete *M. viridis* has negative effects on growth and mortality of the native amphipod *M. affinis*. If food competition occurs we expect to observe reduced growth of the amphipods in the presence of the

polychaetes at elevated food level, whereas we would attribute negative effects in the presence of the polychaetes at severely limited food resources to other interference mechanisms (e.g. direct damage or predation). We were interested in testing the effect of the polychaetes on the amphipods at conditions similar to the deeper parts of the northern Baltic Sea. Therefore our experiment included one food level equivalent to spring bloom (and a no-food control), the field densities of amphipods (three levels for both juveniles and adults) and polychaetes (one level and a zero control).

2. Material and methods

The experiment was carried out at the Askö laboratory in the north-western Baltic Sea proper (58°49' N, 17°34' E). Altogether 120 microcosms were used to permit 24 treatments replicated 5 times. Two year classes (0y+, 1y+) of *M. affinis* were kept at average, high and very high densities and *M. viridis* was added at zero and high densities typical of deep soft bottoms of the northern Baltic Sea. The microcosms were seeded with a mixture of algae (see below) or left without food (Table 1).

Sediment and *M. affinis* used in the experiment were sampled at a 28-m-deep muddy station in the vicinity of the laboratory. Prior to the onset of the spring bloom (10 March 1999), sediment samples were taken with a van Veen grab. The sediment (muddy silt) was sieved through a 300 µm mesh to homogenise it and to remove all macrofauna. It was stored aerated at 7 °C in the dark (to keep photosynthetic processes at minimum). *M. affinis* were collected with a benthic sledge (Blomqvist and Lundgren, 1996) 4 days before the start of the experiment. The sediment was immediately sieved through 1 and 0.5 mm sieves and 1-y-old (1y+) and juveniles of *M. affinis* (0y+) were picked up in batches of 10 with a small piece of nylon net.

In 1999 *M. viridis* was found in very few localities in the Askö area and the densities were too low to satisfy the purpose of our experiment. Therefore, *M. viridis* were collected from the Greifswalder Bodden, southern Baltic Sea (54°09' N, 13°38' E) where the worms occurred at high densities. The specimens of *M. viridis* in Greifswalder Bodden and Askö areas are

Table 1

Experimental setup of investigating the effect of *Marenzelleria viridis* on 0y+ (juv) and 1y+ (ad) *Monoporeia affinis* at different population densities (ind per microcosm) and food regimes

Treatment	<i>M. affinis</i>		<i>M. viridis</i>	Food added
	Density	Age	Density	
1	20	ad	2	yes
2	20	ad	2	no
3	20	juv	2	yes
4	20	juv	2	no
5	40	ad	2	yes
6	40	ad	2	no
7	40	juv	2	yes
8	40	juv	2	no
9	80	ad	2	yes
10	80	ad	2	no
11	80	juv	2	yes
12	80	juv	2	no
13	20	ad	0	yes
14	20	ad	0	no
15	20	juv	0	yes
16	20	juv	0	no
17	40	ad	0	yes
18	40	ad	0	no
19	40	juv	0	yes
20	40	juv	0	no
21	80	ad	0	yes
22	80	ad	0	no
23	80	juv	0	yes
24	80	juv	0	no

In order to obtain the densities per m² the values should be multiplied by 100. Five replicates were analysed for each treatment.

considered to belong to the same population, originating from the same introduction event (Essink, 1999). The polychaetes were sampled from a silty-sand bottom at 2 m depth on 16 April and held aerated with sediment at 7 °C (both during transportation and storing at the Askö laboratory). The salinity in Greifswalder Bodden and Askö area was similar (~ 6 PSU).

Prior to the start of the experiment, the sediment was thoroughly mixed to ensure homogeneity. Cylindrical plastic jars (100 cm²) were filled with a 6 cm layer of sediment and a 6 cm layer of water (Fig. 1) and allowed to settle for 24 h. Then polychaetes (mean length 62 ± S.E. 2 mm) were randomly chosen and added to the microcosms at densities (200 m⁻²) that correspond to the high field abundances as found in the deeper parts (>10 m) of the northern Baltic Sea. This was done to increase the chances of detecting any possible negative effects at field levels.

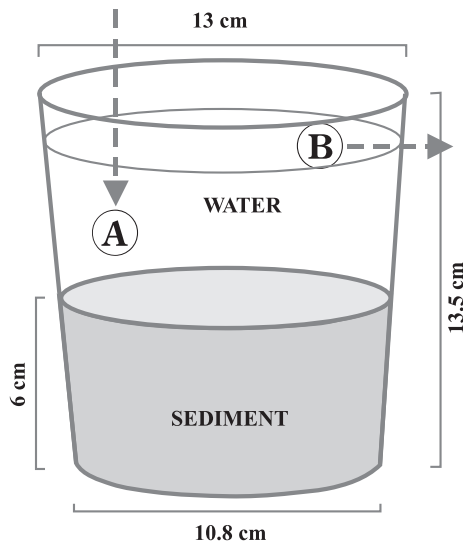


Fig. 1. Experimental setup of microcosms. (A) 20 μm mesh, (B) 200 μm mesh. Arrows show the direction of water flow.

One day later (30 April) *M. affinis* were added to the microcosms (juveniles: mean length 1.71 ± 0.02 , mean dry weight (60 °C, 48 h) $61 \pm 10 \mu\text{g}$, adults: mean length 6.38 mm, mean dry weight $975 \pm 40 \mu\text{g}$). The microcosms were supplied with cooled filtered (20 μm) seawater from 16 m depth (temperature 6.6 °C, salinity 6.0 PSU) at an average flow rate of around $25 \text{ cm}^3 \text{ min}^{-1}$. The experiment was carried out in the dark.

The animals were fed with diatoms over three weeks to imitate field conditions as far as possible. A mixture of *Skeletonema costatum* (Greville) Cleve (60%), *Nitzschia closterium* (Ehrenberg) W. Smith (30%) and other algae (10%) was used. The algae were cultured at 15 °C in artificial seawater (Kester et al., 1967) at a salinity of 15 PSU with added nutrients, trace metals and vitamins (Guillard, 1975). Prior to food addition, the salinity of the culture was lowered to 6–7 PSU by using filtered seawater. To facilitate algal settlement, the water flow through the jars was stopped for 5 h during the feeding procedure. The food was given on average twice a week (1 g C m^{-2} per feeding). A water sample for the culture was taken, filtered on Whatman CF/F filter, and analysed for the carbon content. The feeding procedure was carried out until the amount of food reached spring bloom sedimentation values typical of the Askö area ($5\text{--}8 \text{ g C m}^{-2}$) (Larsson et al., 1986).

At the end of the experiment (64 days) animals were sieved out of the sediment using a 300 μm net. Living animals were counted and preserved in a 4% formaldehyde solution of 6 PSU filtered seawater. The lengths of all polychaetes and 20 randomly chosen amphipods in each microcosm were measured by camera lucida using a light microscope.

Because of the relatively high mortality rate of the polychaetes (40%) at the end of the experiment, all jars containing dead polychaetes were omitted from statistical analyses. Some treatments had less mortality, but to keep the design balanced (Underwood, 1997) two replicate jars of each treatment without polychaetes were omitted randomly resulting in 3 replicate jars of each treatment. Analyses of variance (ANOVA) were performed to separate the effects of density and food addition on amphipod growth, with and without the polychaete. The power of the tests was assessed by calculating Φ^2 and extrapolated from operating characteristic curves for fixed effects in the ANOVA using the procedure in Montgomery (1991). Length and weight data of *M. affinis* were log (x) transformed while mortalities (proportions) were arcsine transformed. Bartlett's test was carried out prior to the analyses and the results confirmed the assumption of homoscedasticity (Sokal and Rohlf, 1981).

3. Results

3.1. Growth in length

Food, density of amphipods and the presence of the polychaetes had a significant effect on the growth of amphipods. There was also a significant difference in growth between juveniles and adults (4-way ANOVA, Food: $p < 0.001$, Age: $p < 0.001$, Density: $p < 0.05$, *Marenzelleria*: $p < 0.05$, Age \times Food: $p < 0.001$, Fig. 2, Table 2). Growth was significantly higher in microcosms where food was added except for the treatments with 20 1-y-old (1y+) amphipods and *M. viridis*. No significant differences were observed in juvenile (0y+) growth at different amphipod densities and between the treatments where *M. viridis* was present or absent. The 1y+ growth was density-dependent in the absence of the polychaetes and not so in the presence of the polychaetes, though this was significant only at

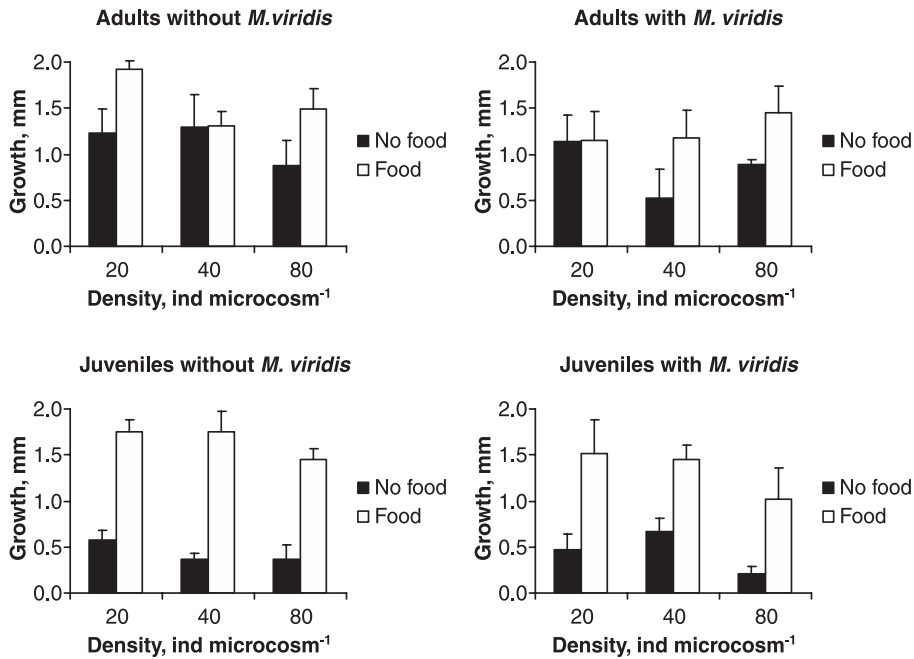


Fig. 2. Mean growth in length (\pm SE) of *Monoporeia affinis* in relation to food availability, amphipod density and presence of *Marenzelleria viridis*.

$p = 0.056$ in a three way analysis of the variance (Table 2). At low densities (20 ind per microcosm) and with food addition, the 1y+ amphipods grew faster in the

absence of the polychaetes than in their presence. The polychaetes did not grow significantly during the course of experiment (ANOVA, $p > 0.05$).

Table 2
Summary of the ANOVA analyses on the growth (length) of the amphipods

Degrees of freedom				
Factor	Effect	Error	F	p-level
<i>4-way ANOVA: Both age classes</i>				
1	1	50	4.8	0.033
2	2	50	3.4	0.040
3	1	50	3806	0.000
4	1	50	93	0.000
3 \times 4	1	50	45	0.000
<i>3-way ANOVA: Adults</i>				
1	1	25	4.0	0.056
2	2	25	1.3	0.297
3	1	25	8.1	0.008
<i>3-way ANOVA: Juveniles</i>				
1	1	25	1.9	0.185
2	2	25	3.8	0.036
3	1	25	90	0.000

Factors 1: *Marenzelleria* densities, 2: *Monoporeia* densities, 3: Food, 4: Age class. Only significant interactions are shown.

3.2. Growth in weight

The results of the growth in weight were similar to growth in length. However, significant effects of *Marenzelleria* were not observed as p values for the 4 and 3 way ANOVA were 0.078 and 0.117, respectively.

3.3. Survival

The survival of amphipods was significantly affected by food addition and there was a difference between year classes. The survival was not affected by amphipod density or the presence of the polychaetes (4-way ANOVA, Food: $p < 0.05$, Age: $p < 0.001$, Density: $p > 0.05$, *Marenzelleria*: $p > 0.05$, interaction terms not significant). When food was available 84% of the 1y+ and 50% of the 0y+ amphipods survived the 64-d experimental period. When no food was added the survival of 1y+ and 0y+ amphipods was lower: 73% and 35%, respectively.

4. Discussion

The results of this experiment indicate that *M. viridis* had a significant effect on the growth of 1y+ *M. affinis* when amphipod density was kept at an average level (200 ind m⁻²) in the presence of an optimal food level, i.e. equivalent to typical carbon values for the spring bloom sedimentation in the Askö area. When amphipod densities were higher *M. viridis* had no effect on *M. affinis*. At higher amphipod densities the food levels were probably always highly suboptimal regardless of the presence of the polychaetes. Hence, the chances of detecting the interspecific food competition between the test animals were reduced. However, when food was given, *M. viridis* had no effect on 0y+ *M. affinis* regardless of amphipod density. Slightly reduced amphipod growth in the presence of the polychaetes (though statistically non-significant) suggests food excess in these treatments during the whole experiment. While we found a statistically significant difference in growth in length of the amphipods in treatments with and without the worms in the 4-way ANOVA, this was not so clear in the 3-way ANOVAs where the p-value was slightly above the critical value of 0.05 for adults and well above this value for the juveniles, viz. 0.185 (Table 2). Adults and juveniles showed ca 60 and 13% more increase in length, respectively, in the treatments with food and at low amphipod density in the absence of the worms than in their presence. Together with the results from the 3-way ANOVA, which is obviously less powerful to detect difference compared to the 4-way ANOVA (see Underwood, 1997), this indicates that the worms mainly affected the growth of adults. The increase in the p-value from 0.033 to 0.078 when weight is analysed instead of length is likely to be caused by less homogenous values because weighings were based on only one measurement while the length was based on mean values of 20 individuals for each replicate. It is likely that the presence of *M. viridis* decreases the chances of individual adult amphipods to make use of the available food resource. Although our experiment did not demonstrate a direct effect of *M. viridis* on the mortality of *M. affinis*, the polychaete may still indirectly, through the reduction of growth, influence the population dynamics of amphipods. The reduction in the growth of amphipods seems to prolong its generation time (Leonardsson

et al., 1988) and reduce its fecundity (Cederwall, 1977). Hence, the competitive interaction between *M. viridis* and *M. affinis* is expected to change the duration of the amphipod's life cycle. Besides, higher macrozoobenthos densities may induce higher swimming activity of *M. affinis* (cf. Lindström and Fortelius, 1990). Consequently, amphipods are longer exposed to possible predation and, hence, population size is likely to diminish.

The intraspecific competition for food between the amphipods was important in the treatments without *M. viridis*. The addition of food increased the growth rates and decreased the mortalities of amphipods. At higher densities the effect was less pronounced. Like Wenngren and Ólafsson (2002) we found in some jars, however, increased juvenile mortalities associated with the food addition. Because *M. affinis* is known to be sensitive to low oxygen concentrations (Johansson, 1997), this pattern was probably related to the temporal hypoxia following the decomposition of surplus organic matter. The rates of amphipod growth and mortality estimated in this study are in accordance with the values reported in Wenngren and Ólafsson (2002). The intraspecific competition for food has previously been documented within and between different year classes of *M. affinis* (Hill, 1992; Elmgren et al., 2001; Wenngren and Ólafsson, 2002) and was considered to be the main mechanism regulating the population size in the field (Sarvala, 1986; Leonardsson, 1994).

During this study we did not observe a significant growth of *M. viridis*. Low and insignificant growth rates may have been due to the fact that we used adult polychaetes and their initial length showed relatively high variability.

The high mortality of the polychaetes in the experimental jars (40%) is a cause of concern. We omitted practically all jars where mortality occurred, resulting in a considerable reduction in total degrees of freedom in the 4-way ANOVA. This had little effect on the power of detecting a difference of 20% in length of 1y+ at alpha levels of 0.05, which remained high. One could argue that the remaining worms were in bad condition and therefore not capable of exerting negative effects on the amphipods. This was found unlikely for two reasons. Firstly, monitoring of the jars indicated that the sediment surface in jars without polychaete mortality showed signs of bioturbation,

with distinct faecal casts on the surface sediment. This was not observed in those jars where the two specimens of *M. viridis* had died. Secondly, at the end of the experiment surviving polychaetes showed high vitality, with fast movements and escape behaviour. Further, the state of those individuals that had died indicated that this must have happened early in the experiment as their tissue was largely decomposed.

Another limitation of our experiment was the thickness of the sediment in the microcosms. Since *M. viridis* is a deep-burrowing polychaete (Hines and Comtois, 1985), too thin sediment layers may increase the probability of encounters and interactions between the test animals. However, in the deep soft-bottom habitats of the northern Baltic Sea it is likely that, owing to reduced oxygen concentrations (e.g. Kube and Powilleit, 1997) and increasing clay content, *M. viridis* does not penetrate very deep into the sediment.

Competitive interactions for food between *M. viridis* and *M. affinis* may be more intense in eutrophicated and/or shallower areas where the density of the polychaete often reaches over 3000 ind m⁻² during the later successional stages (Zettler, 1997). In the Dollard (The Netherlands), however, Essink et al. (1998) and Essink (1999) found considerable increase in macrozoobenthic biomass after the introduction of *M. cf. wireni*. They suggest that the polychaete was filling an unused space, therefore not affecting the resident fauna in other niches. Ever since the invasion of *M. cf. viridis* in the Gulf of Riga (NE Baltic Sea), the abundance of *M. affinis* has decreased notably in the deeper areas but increased in the shallower areas (Cederwall et al., 1999). They conclude that the collapse of *M. affinis* in deeper sites of the Gulf of Riga was primarily related to oxygen deficiency. The densities of *M. viridis* were estimated at less than 500 ind m⁻² and the polychaetes were not considered to affect the native fauna. However, in recent years with good oxygen regime and increasing densities of *M. viridis*, no recovery of *M. affinis* has been observed in the Gulf (Database of the Estonian Coastal Monitoring). This suggests stronger competitive interactions between the species in the deeper areas while other factors (e.g. unlimited food sources, interactions with other species) may release amphipods from such competition in the shallow water (Kotta et al., 2001).

To conclude, our experiment suggests that *M. viridis* is able to reduce the growth of *M. affinis* in the deep soft-bottom habitats in the northern Baltic Sea. This negative effect may be attributed to food competition rather than to other mechanisms of interference competition.

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