Estonian Journal of Ecology, 2009, **58**, 4, 324–331 doi: 10.3176/eco.2009.4.07

Food competition between the benthic polychaete *Hediste diversicolor* and the semipelagic mysid *Neomysis integer* in the northern Baltic Sea

Helen Orav-Kotta✉, Jonne Kotta, and Ilmar Kotta

Estonian Marine Institute, University of Tartu, Mäealuse 10a, 12618 Tallinn, Estonia
✉ Corresponding author, helen.orav@sea.ee

Received 12 February 2009, revised 9 June 2009

Abstract. To date, there are virtually no studies where the competitive interactions between benthic and pelagic species are experimentally evaluated although such benthic–pelagic coupling might be relevant in many instances. In this study we investigated if *Hediste diversicolor* and *Neomysis integer* compete with each other for space and food during May–June when the densities of both species are very high in the shallow bays of the northern Baltic Sea. The interspecific interactions between the test organisms were studied in small plastic buckets placed on the seafloor in a shallow (2 m) bay. Experiments showed that *H. diversicolor* was competitively superior over *N. integer*. At a low food level the competitive interactions reduced the survival of *N. integer* whereas at a high food level no such negative effects were observed.

Key words: Baltic, benthic–pelagic coupling, field experiment, interspecific interaction.

INTRODUCTION

As the structure of benthic communities in the Baltic Sea is relatively simple, the area offers a unique opportunity to study the mechanisms and detect the driving forces of changes in biodiversity. Nevertheless, scientists are still debating about the relative contribution of biotic interactions and physical disturbance in determining the patterns of coastal communities in the northern Baltic Sea. Earlier studies demonstrated significant intra- and interspecific competitive links among several benthic algal and invertebrate species in the region (Kotta et al., 2001, 2008; Orav-Kotta et al., 2009). Other studies, however, supported an alternative view that physical disturbance is the main mechanism of community dynamics in the northern Baltic Sea region (e.g. Kautsky & van der Maarel, 1990; Herkül et al., 2006).

Earlier studies have focussed on the competitive links either between benthic or pelagic species. To date, there are virtually no studies where the competitive interactions between benthic and pelagic species are experimentally evaluated although such benthic–pelagic coupling might be relevant in many instances.

Neomysis integer (Leach) is the most prevalent mysid species in the coastal areas of the northern Baltic Sea (Kotta & Kotta, 1999). In May–June the bulk of the population is concentrated in the shallow areas below the 10 m depth. In the less exposed bays the density of mysids may occasionally exceed 10 000 ind. m^{-2}.

It is likely that in such shallow areas the density of plankton is low and the food should be primarily obtained from the upper layer of the sediment. *Neomysis integer* is considered to be omnivorous. It is known to feed besides phytoplankton and zooplankton on bottom detritus and filamentous algae (Mauchline, 1971). The polychaete *Hediste diversicolor* (O. F. Müller) is the key benthic invertebrate species in these shallow and isolated bays. The species is a deposit feeder at juvenile stages and a predator at the later stages of its development (Bonsdorff & Pearson, 1999). Hence, competition between the species is likely in these areas.

The aim of this study was to investigate if the two species are competing for space and food during May–June when the densities of both species are very high in the shallow bays. We expect that at low food levels the competitive interactions reduce the growth and survival of the test organisms whereas at high food levels such negative effects do not occur.

MATERIAL AND METHODS

The in situ food competition between the prevalent mysid *N. integer* and the polychaete *N. diversicolor* was studied in a shallow (2 m) bay (59°50 ′N, 23°15 ′E) adjacent to the Tvärminne Zoological Station in the north-eastern Baltic Sea. The bay is moderately exposed to the sea and the prevailing sediment is silty sand. The test organisms and sediment were collected in the vicinity of the experimental site. The sediment was sieved through a 1 mm mesh and dried in the sun for 3 days to assure that it was free from living benthic invertebrates.

To investigate interspecific interactions between the test organisms, 3 L plastic buckets (Ø 18 cm) were used. The buckets were filled with an 8 cm layer of sediment and a 7 cm layer of seawater and allowed to settle for 6 h. The test organisms were added to four replicate buckets per treatment (totalling 24 buckets). Four individuals of *H. diversicolor* and/or 15 individuals of *N. integer* were added to each bucket so that their densities corresponded to natural densities in the study area. The animals were fed by adding sediment rich in detritus and microphytobenthos. A more detailed setup of the experiment is given in Table 1. The buckets were closed by a mesh-net (0.2 mm mesh size) to minimize the risk of migration but at the same time to assure sufficient water exchange in the buckets.

Table 1. Experimental setup. Abundance (individuals per bucket) and feeding regime (fed or not fed) are given

Treatment	Species	Abundance	Feeding
1	*Hediste diversicolor*	4	No
2	*Neomysis integer*	15	No
3	*Hediste diversicolor* + *Neomysis integer*	4 + 15	No
4	*Hediste diversicolor*	4	Yes
5	*Neomysis integer*	15	Yes
6	*Hediste diversicolor* + *Neomysis integer*	4 + 15	Yes

The experimental buckets were randomly placed on the seafloor at a depth of 0.5 m. The average distance between the buckets was 0.5 m. The experiment lasted for 18 days. The mesh-net was cleaned once a day to avoid clogging. Oxygen conditions were regularly measured outside and inside the buckets. No oxygen deficiency was detected within the control buckets with no macrofauna (minimum 6.2 mg L^{-1}, average 9.4 mg L^{-1}). Prior to the experiment, 20 individuals of each studied species (representing the same cohort as used in the experiment) were randomly selected and their dry weight (80 °C, 48 h, ±0.001 g) was determined. In addition, the length (±0.1 mm) of *N. integer* was measured. At the end of the experiment, sediment was sieved (300 µm mesh-net) and test organisms were counted. The dry weight values of all experimental animals and the length of *N. integer* were determined. The survival was estimated as the difference in the density of test organisms per bucket between the beginning and the end of the experiment.

Repeated measures ANOVA (StatSoft, 2008) was used to compare the effect of food addition (levels: added, not added) and species (levels: *H. diversicolor* or *N. integer*) on species survival and growth among single (*H. diversicolor* or *N. integer*) and two-species treatments (*H. diversicolor* and *N. integer*). Repeated measures ANOVA was used here as the experimental treatments did not follow the assumption of independence, i.e. the requirement for standard ANOVA. Namely, the two studied species of benthic invertebrates in each bucket are not independent and should be treated as repeated measures. The Mauchly Sphericity test was used to check the assumption of equality of variance. We used the following multivariate tests to seek the statistical significance of food addition and species on the survival and growth of the test organisms: Wilks' lambda, Pillai-Bartlett trace, and Hotelling-Lawley trace tests. These tests were used as they do not make the strict, often unrealistic, assumptions about the structure of the covariance matrix. As all these tests resulted in similar significances, only the output of Wilks' lambda test (as the most commonly used) is reported. Post-hoc Bonferroni tests were used to analyse which treatment levels were statistically different from each other.

RESULTS

At the beginning of the experiment, the average length of *N. integer* and *H. diversicolor* was 11.2 and 60 mm and the average weight was 0.0016 and 0.0200 g dw, respectively. Our experiments showed that the survival of *N. integer* was lower in the treatments with no food addition compared to treatments when food was added. The difference was mainly due to the presence of *H. diversicolor* as no negative effect of low food levels on the species survival was observed in the treatments with *N. integer* alone (Table 2, Fig. 1).

On the other hand, the experiments demonstrated that food addition had no effect on the growth of *N. integer* and *H. diversicolor* calculated either on length or weight basis. Similarly, the presence of the competitor had no effect on the growth of the species as there were no statistical differences in the growth rates among treatments with single and two species communities (Figs 2, 3).

Table 2. Multivariate tests of significance of repeated measures ANOVA to compare the effect of species (levels: *N. integer*, *H. diversicolor*) and food addition (levels: added, not added) on the survival and growth of test animals among single (*N. integer* or *H. diversicolor*) and two-species treatments (*N. integer* and *H. diversicolor*). Probability values in bold denote significant effects of factors and interactions

Effect	Wilks' test value	*F*	*p*
SURVIVAL			
Intercept	0.0005	11 401.82	0.000
Species	0.4239	7.47	**0.009**
Food addition	0.5714	4.12	**0.046**
Species × Food addition	0.5714	4.12	**0.046**
GROWTH IN LENGTH			
Intercept	0.3030	12.65	0.001
Species	0.3379	10.78	**0.003**
Food addition	0.9826	0.10	0.908
Species × Food addition	0.9816	0.10	0.903
GROWTH IN WEIGHT			
Intercept	0.3771	9.08	0.005
Species	0.3978	8.33	**0.006**
Food addition	0.8479	0.99	0.403
Species × Food addition	0.8350	1.09	0.371

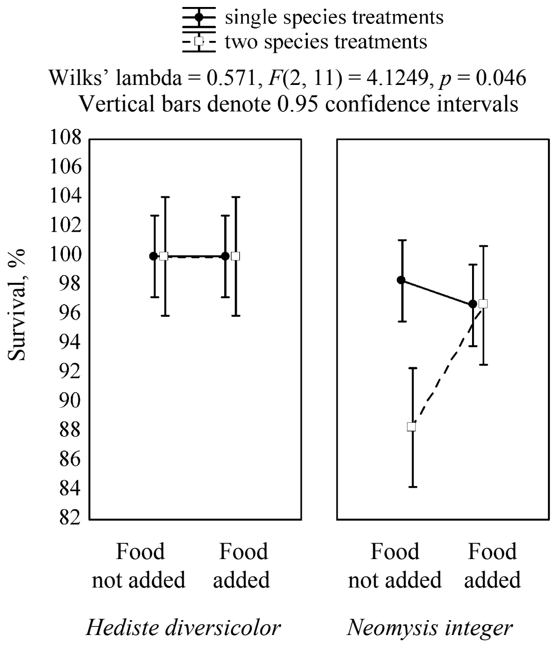

Fig. 1. Changes in the survival of *N. integer* and *H. diversicolor* at different treatments.

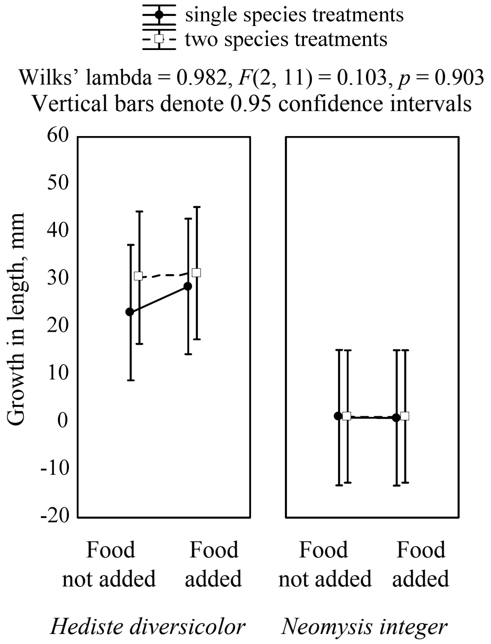

Fig. 2. Changes of the growth in length of *N. integer* and *H. diversicolor* at different treatments.

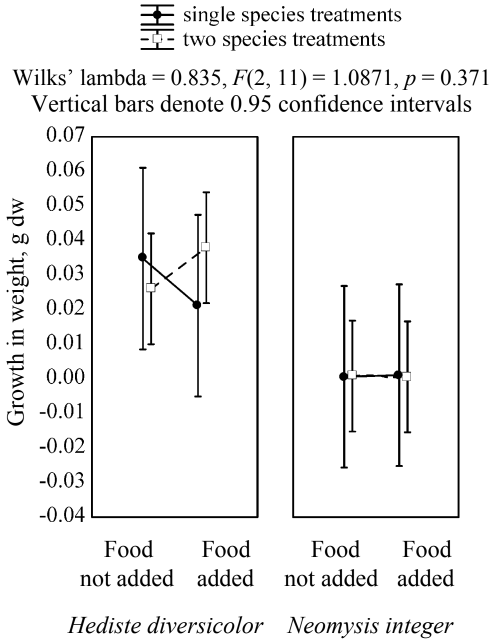

Fig. 3. Changes of the growth in weight of *N. integer* and *H. diversicolor* at different treatments.

DISCUSSION

The results of this study were in accordance with our prediction that at low food levels the competitive interactions would reduce the survival of the test organisms whereas at high food levels no such negative effects would be observed. Our study also demonstrated that *H. diversicolor* was competitively superior to *N. integer*.

This corroborates earlier observational and experimental studies showing that macrofaunal communities are often food limited in many soft bottom habitats (e.g. Brey, 1991; Kotta et al., 2007). Earlier studies also point out that both *H. diversicolor* and *N. integer* compete with other invertebrates for food and space (Wilson, 1990; Kotta et al., 2001; David et al., 2005).

Our study is the first manipulative experiment that reports interspecific competition for food between the benthic deposit-feeding polychaete and the semipelagic mysid species. It is possible that the mechanism behind the negative effect of *H. diversicolor* on *N. integer* is indirect. The polychaete seems to be able to search for detritus at a higher rate and at a much wider surface area than the mysid. The outcome of such behaviour explains the reduced survival of *N. integer* in the presence of *H. diversicolor*. 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 *H. diversicolor* 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 to food shortages.

Alternatively, it is also plausible that the mechanism behind the negative effect of *H. diversicolor* on *N. integer* is a direct aggression of *H. diversicolor* on *N. integer*. As *H. diversicolor* is known to be an aggressive predator (Witte & De Wilde, 1979; Ólafsson & Persson, 1986; Rönn et al., 1988) its negative effect on *N. integer* is expected when food is limiting the growth of the species. Moreover, *H. diversicolor* is known to interfere negatively or even kill other polychaete species (Witte & De Wilde, 1979) although it is competitively inferior to the invasive polychaete *Marenzelleria neglecta* (Kotta et al., 2001). The polychaete also interacts with amphipods by a combination of aggressive predation, interference, and disturbance (Ólafsson & Persson, 1986; Rönn et al., 1988).

To conclude, the overall aim of this experiment was to shed further light on competitive interactions that regulate marine benthic biodiversity in the northern Baltic Sea. The study showed competition of *N. integer* and *N. diversicolor* for food in shallow eutrophicated bays of the northern Baltic Sea. Under poor food conditions, *N. diversicolor* induced additional mortality to *N. integer* whereas *N. integer* had no such negative effect on *H. diversicolor*.

ACKNOWLEDGEMENTS

The work was supported by the Walter and Andrée de Nottbeck Foundation, target-financed projects SF0180013s08 of the Estonian Ministry of Education and Research, and Estonian Science Foundation grants 6015, 6016, and 7813. Sincere thanks are due to the staff of Tvärminne Zoological Station.

REFERENCES

Bonsdorff, E. & Pearson, T. H. 1999. Variation in the sublittoral macrozoobenthos of the Baltic Sea along environmental gradients: a functional-group approach. *Aust. J. Ecol.*, **24**, 312–326.

Brey, T. 1991. Interactions in soft bottom benthic communities: quantitative aspects of behaviour in the surface deposit feeders *Pygospio elegans* (Polychaeta) and *Macoma balthica* (Bivalvia). *Helgoland Mar. Res.*, **45**, 301–316.

David, V., Sautour, B., Chardy, P. & Leconte, M. 2005. Long-term changes of the zooplankton variability in a turbid environment: the Gironde estuary (France). *Estuar. Coast. Shelf Sci.*, **64**, 171–184.

Herkül, K., Kotta, J., Kotta, I. & Orav-Kotta, H. 2006. Effects of physical disturbance, isolation and key macrozoobenthic species on community development, recolonisation and sedimentation processes. *Oceanologia*, **48S**, 267–282.

Kautsky, H. & van der Maarel, E. 1990. Multivariate approaches to the variation in benthic communities and environmental vectors in the Baltic Sea. *Mar. Ecol. Prog. Ser.*, **60**, 169–184.

Kotta, I. & Kotta, J. 1999. Distribution and migration of mysids in the Gulf of Riga (northern Baltic). *Proc. Estonian Acad. Sci. Biol. Ecol.*, **48**, 284–295.

Kotta, J., Orav, H. & Sandberg-Kilpi, E. 2001. Ecological consequence of the introduction of the polychaete *Marenzelleria viridis* into a shallow water biotope of the northern Baltic Sea. *J. Sea Res.*, **46**, 273–280.

Kotta, J., Lauringson, V. & Kotta, I. 2007. Response of zoobenthic communities to changing eutrophication in the northern Baltic Sea. *Hydrobiologia*, **580**, 97–108.

Kotta, J., Paalme, T., Kersen, P., Martin, G., Herkül, K. & Möller, T. 2008. Density dependent growth of the red algae *Furcellaria lumbricalis* and *Coccotylus truncatus* in the West-Estonian Archipelago Sea, northern Baltic Sea. *Oceanologia*, **50**, 577–585.

Mauchline, J. 1971. The biology of *Neomysis integer* (Crustacea, Mysidacea). *J. Mar. Biol. Assoc. U.K.*, **51**, 347–354.

Ólafsson, E. B. & Persson, L.-E. 1986. The interaction between *Nereis diversicolor* O. F. Müller and *Corophium volutator* Pallas as a structuring force in a shallow brackish sediment. *J. Exp. Mar. Biol. Ecol.*, **103**, 103–117.

Orav-Kotta, H., Kotta, J., Herkül, K., Kotta, I. & Paalme, T. 2009. Seasonal variability in the grazing potential of the invasive amphipod *Gammarus tigrinus* and the native amphipod *Gammarus salinus* in the northern Baltic Sea. *Biol. Invasions*, **11**, 597–608.

Rönn, C., Bonsdorff, E. & Nelson, W. G. 1988. Predation as a mechanism of interference within infauna in shallow brackish water soft bottoms; experiments with an infauna predator, *Nereis diversicolor* O. F. Müller. *J. Exp. Mar. Biol. Ecol.*, **116**, 143–157.

StatSoft, Inc. (2008). STATISTICA (data analysis software system), version 8.0. www.statsoft.com.

Wilson, W. H. 1990. Competition and predation in marine soft-sediment communities. *Annu. Rev. Ecol. Syst.*, **21**, 221–241.

Witte, F. & De Wilde, P. A. W. J. 1979. On the ecological relation between *Nereis diversicolor* and juvenile *Arenicola marina*. *Neth. J. Sea Res.*, **13**, 394–405.

Toidukonkurents bentilise hulkharjasussi *Hediste diversicolor*'i ja semipelaagilise müsiidi *Neomysis integer*'i vahel Läänemere põhjaosas

Helen Orav-Kotta, Jonne Kotta ja Ilmar Kotta

Tänaseni puuduvad konkurentsialased uuringud bentiliste ja pelaagiliste suurselgrootute vahel, ehkki sellised interaktsioonid võivad paljudes meredes olulised olla. Eksperimentaalselt on uuritud, kas esineb toidu- ja ruumikonkurentsi *Hediste diversicolor*'i ning *Neomysis integer*'i vahel mais-juunis, kui mõlema liigi arvukus on Läänemere rannikumere madalamates osades suur. Katseloomadevahelist konkurentsi uuriti plastmassämbrites, mis paigutati madalaveelise (2 m) merelahe põhja. Eksperimendid näitasid, et *H. diversicolor* oli konkurentsis *N. integer*'ist oluliselt üle. Toidunappuse korral põhjustas *H. diversicolor N. integer*'i suuremat suremust, samas kui toidukülluse korral sellist negatiivset mõju ei täheldatud.