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The influence of *Hediste diversicolor* (O.F. MÜLLER, 1776) on the macro- and meiozoobenthos of a shallow water area of Mecklenburg Bay (Western Baltic Sea)

Introduction

The purpose of many ecological studies is to identify interactions between faunistic ecosystem components by means of laboratory and field experiments. It has often been shown that abiotic and biotic factors such as competition, disturbance and predation influence the composition and dynamics of macrobenthos communities (REISE, 1977; COMMITO and AMBROSE, 1985; AMBROSE, 1986; BEUKEMA, 1987; KIKUCHI, 1987; REDMOND and SCOTT, 1989; COMMITO and BANCAVAGE, 1989; MATILA and BONSDORFF, 1989; HILL et al., 1990).

Experiments have also been performed to detect interactions between macrofauna and meiofauna (BELL & Coull, 1978; REISE, 1979; GEE et al., 1985; ALONGI and TENORE, 1985).

The interactions between Nereidae and infauna that are common in shallow water and are fairly easily handled have been a major topic of study (COMMITO, 1982; REISE, 1979b; COMMITO and SCHRADER, 1985; OLAFSON and PERSSON 1986; RÖNN et al., 1988).

The purpose of our studies was to investigate the influence of the omnivorous *H. diversicolor* on the infauna of a shallow water region in the southern Baltic Sea. *H. diversicolor* achieves abundances of between 5,000 and 15,000 ind · m⁻² (individual dominances up to 15 %) in the investigation area and is thus a major component of the macrofauna. It therefore seemed likely that its carnivorous feeding habits can affect community structure.

To detect direct influences on both the macrozoobenthos and meiozoobenthos and to reduce box effects, we performed short term experiments. ,

Investigation area

The investigation area is situated in a relatively sheltered shallow region in the southern part of Mecklenburg Bay (Fig. 1). Wind-induced water level fluctuations never exceeded 1 m during the experiments and were superimposed on the regular tidal range of about 0.2 m. Water temperatures were subject to normal fluctuations; they rose to 22° C in summer and dropped to about 0° C

in winter. The salinity varied between 10.5 ‰ in summer and 16.5 ‰ in winter. The boxes used for the experiments were about 50 m from the shore, where the water was about 0.5 m deep. The sediment was mineral in character, and its mean grain size varied from 0.23 to 0.31 mm. The water content of the sediment was about 25 %ww. Its organic content varied seasonally, reaching 1.5 % dw in late summer and dropping to 0.4 % dw in winter. The characteristic macrozoobenthos species of the region were *Hydrobia ventrosa*, *Hediste diversicolor* and *Corophium volutator*. They achieved mean individual dominances of around 80 %.

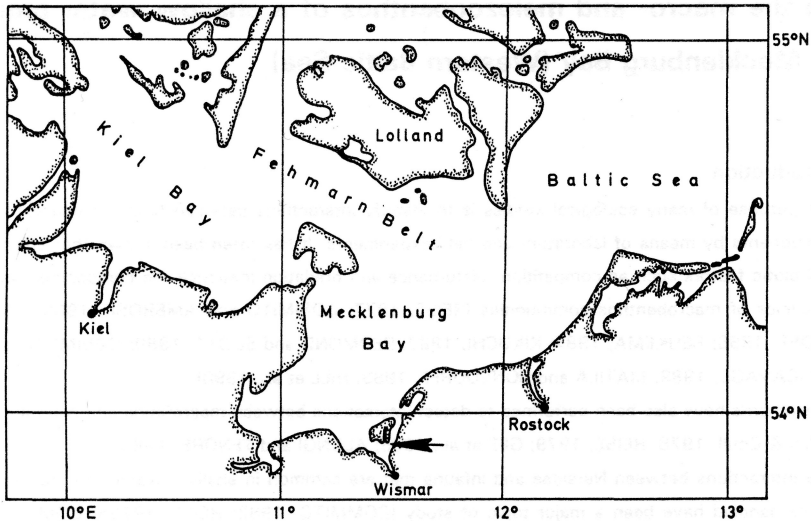


Fig. 1 Investigation area (arrow) in Mecklenburg Bay

Material and methods

Four box experiments were performed from April to September to investigate the direct influence of *H. diversicolor* on the macrofauna and meiofauna. The boxes consisted of PVC tubes. The diameter of the box used for experiment 1 was 19.5 cm (about 300 cm²). Boxes with a diameter of 10.5 cm (about 87 cm²) were used for experiments 2 to 4.

The boxes were pushed into the sediment to a depth of 20 to 25 cm by carefully turning and pressing them to avoid disturbing the presediment as far as possible. The top edges of the boxes were 10 to 15 cm above the sediment surface after installation.

After a defined number of *H. diversicolor* of alength of 15 - 50 mm (Table 1) had been placed in each box, the boxes were covered with gauze (mesh size: 0.1 mm). Inspection at the end of the experiment revealed that the entire gauze had been colonized by microflora and microfauna, but water exchange was still possible through pores that had not become completely clogged.

Table 1 Number of added *H. diversicolor* specimens
0 = natural stocking density ($\bar{x}$ = ind 10 cm⁻²)

	B1		B2		0
	total	$\bar{x}$	total	$\bar{x}$	$\bar{x}$
experiment 1	300	10.0	600	20.1	4.4
experiment 2	80	9.2	160	18.5	4.4
experiment 3	60	6.9	120	13.8	7.3
experiment 4	45	5.2	90	10.4	17.0

Three boxes were used for each experiment. One box (BO) served as a control and was therefore not treated, but was also covered with gauze. The boxes to which a small number of *H. diversicolor* were added were denoted B1, and those in which a larger number of were added were denoted B2. The numbers of these animals added to the different boxes are shown in Table 1. The *H. diversicolor* specimens used for the experiments were collected near the boxes immediately before each experiment began. None of them were visibly injured, and they were all at least 15 mm long.

The quantitative and qualitative composition of the macrozoobenthos and meiozoobenthos was analyzed and the sedimentological and hydrographic parameters measured near the boxes at the beginning and end of the experiments (initial value 0; final values: I, II).

For experiment 1 we analyzed the sediment grain size, water content and organic content in the boxes. The results are presented in Table 2. No significant differences were found inside the boxes after eight weeks, although the organic content of boxes BO to B2 were slightly higher at the end than at the beginning of this period. The low water content values in I and II were doubtless a consequence of the extremely low water level at the time of sampling. All samples (both macrozoobenthos and meiozoobenthos) were collected by means of a corer (about 3 cm², 5 - 6 cm core length). Four cores were combined to form a pooled sample for the second part of experiment 1 and for experiment 3.

Table 2 Sediment characteristics during experiment 1

	03.04.90	03.05.90	28.05.90			
	0	I	II	BO	B1	B2
median grain-size (mm)	0.269	0.234	0.297	0.265	0.191	0.260
water content $\bar{x}$ (% w/w)	25.93	23.75	23.36	25.94	25.38	25.01
SD	0.33	0.26	0.58	0.14	0.43	0.56
organic matter $\bar{x}$ (% dw)	0.73	0.97	0.87	0.93	0.99	0.08
SD	0.12	0.06	0.14	0.06	0.17	0.10

The samples were sieved (mesh size: 0.1 mm) after fixation in 4 % formaldehyde solution. The temporary meiofauna and small oligochaetes such as *Amphichaeta sannio* were examined separately from the permanent meiofauna.

The use of a corer (3 cm²) and a 0.1 mm sieve is rather unusual in macrozoobenthos studies. However, examination of various available sampling techniques showed that this method was very effective in our investigation area, particularly during the period from April to November. A publication dealing with this problem is in preparation.

The results were tested for significant differences by simple analysis of variance after the normality of distribution (zero class test) and homogeneity of variance (BARTLETT test) had been verified. Significant differences between values were identified by DUNCAN's multiple range test.

Results

Macrozoobenthos (Tables 3-6, Fig. 2)

The results of experiments 1 to 4 are summarized in Tables 3 to 6. The results resembled each other in some cases, but others were typical of only one experiment. The data from experiment 2 will not be presented and discussed here because they scarcely permit interpretation (Table 4), especially those from the control box (BO). In the case of this box, only the abundance of *H. diversicolor* is comparable to the controls 0 and I. Apart from hydrobiid snails, especially the oligochaetes exhibited low abundances and achieved only 22.7 % of the individual density of the initial value (0) and 15.8 % of the control value (I). A similar decrease in abundance was found in B1.

The direct influence of *H. diversicolor* on *Corophium volutator* abundance in B1 and B2 was evident in all experiments. In the control boxes BO, the *C. volutator* population developed in the same way as outside (Fig. 2). The statistical analysis of these abundances is shown in Table 8. No statistical analysis was possible for experiment 3 owing to the pooling of samples. However, the results of experiments 1 and 4 were convincingly confirmed (see also Fig. 2). There was a clear difference between the abundances in B1 and B2 only in this experiment. *C. volutator* was thus the only species in our experiment that was subject to a direct negative effect of *H. diversicolor*, at least during the investigation period (April to September).

The population density of *H. diversicolor* in the control boxes BO did not differ significantly from that in control areas I and II in any instance. Nor were significant changes in abundance outside of the boxes observed during the short duration of the experiments, although an increase in colony density was observed between April and September as a result of reproduction (Tables 3-6). The abundance of *H. diversicolor* in the boxes (B1 and B2) to which specimens of this species had been added was naturally higher in all experiments than in the untreated boxes (BO) and was also higher than outside of the boxes (I, II). B1 in experiment 1 (2nd part) was the sole exception

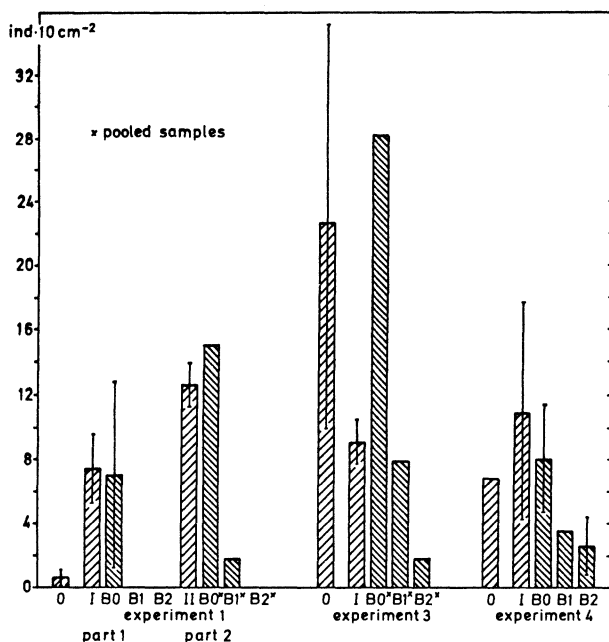


Fig. 2 Abundances ($\bar{x} \pm SD$) of *Corophium volutator* in experiments 1, 3, and 4

- * = pooled samples
- O = surrounding area at the beginning of the experiments
- I = surrounding area during first sampling
- II = surrounding area during second sampling
- BO = untreated box, B1 and B2 see table 1

(Table 3). Strikingly, however, the expected population density (initial value 0 plus the number of additional *H. diversicolor*) was not achieved in any case. In experiment 4 (B1 and B2), the number of individuals did amount to about 90 % of the expected value (Table 6), but in the other experiments the abundances achieved only 55 to 70 % of this theoretical value. The densities in the second part of experiment 1 were particularly extreme in this respect. Only 20 to 30 % of the theoretically expected number of *H. diversicolor* were found in B1 and B2. Since we found hydrobiid snails on the inside of the gauze and on the box sides after opening the boxes, and these had obviously migrated out of the sediment, the hydrobiid values are rather difficult to analyze. However, there was a striking reduction in hydrobia abundance as *H. diversicolor* abundance increased only during the second part of experiment 1 (Table 3).

Table 3 Macrofauna abundances ($\bar{x}$ = ind $\cdot$ 10 cm⁻²) in experiment 1 (see also legend of Fig. 2)

	03.04.1990		03. 05.1990						28.05.1990						
Taxa	O	n=3	I	n=3	BO	n=4	B1	n=4	B2	n=4	II	n=3	BO *	B1 *	B2 *
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	$\bar{x}$	$\bar{x}$
Hydrobiidae	27.6	6.7	27.3	3.9	7.9	1.8	17.6	8.1	39.6	29.8	17.3	2.2	6.2	1.8	18.5
Paranais littoralis	2.1	1.3	2.6	1.8	2.6	3.4	0.9	1.8	0.9	1.8	8.2	1.0	8.8	6.2	3.5
Amphichaeta sannio	-	-	0.3	0.5	1.8	2.0	-	-	-	-	0.9	1.5	0.9	0.9	-
Tubifex costatus	15.3	3.3	15.0	4.7	10.6	4.1	3.5	2.9	15.0	13.3	11.4	3.2	18.5	21.2	15.0
Enchytraeidae	13.5	5.0	26.5	19.9	16.7	12.7	6.2	3.4	7.9	5.3	12.0	3.1	3.5	9.7	3.5
Hediste diversicolor	4.4	1.8	6.5	4.4	3.5	2.9	9.7	3.4	15.9	8.9	5.6	1.9	2.6	3.5	7.1
Manayunkia aestuarina	3.2	0.5	1.5	0.5	3.5	5.0	1.8	2.0	4.4	3.4	1.8	1.5	2.6	6.2	1.8
Corophium volutator	0.6	0.5	7.4	2.2	7.0	5.8	-	-	-	-	12.6	1.3	15.0	1.8	-
Sphaeroma hookeri	0.3	0.5	0.3	0.5	-	-	-	-	-	-	-	-	-	-	-
Chironomidae larvae	0.3	0.5	-	-	-	-	0.9	1.8	-	-	-	-	-	-	-
sum	67.3	6.7	87.3	16.8	53.7	9.3	40.5	13.3	83.6	43.3	70.0	2.8	58.2	51.1	49.4

Table 4 Macrofauna abundances ($\bar{x}$ = ind $\cdot$ 10 cm⁻²) in experiment 2 (see also legend of Fig.. 3)

	03.04.1990				03.05.1990					
T a x a	O $\bar{x}$	n = 3 SD	I $\bar{x}$	n = 3 SD	BO $\bar{x}$	n = 4 SD	B1 $\bar{x}$	n = 4 SD	B2 $\bar{x}$	n = 4 SD
Hydrobiidae	27.6	6.7	27.3	3.9	15.2	8.8	22.2	15.8	26.8	10.7
Paranais littoralis	2.1	1.3	2.6	1.8	-	-	-	-	3.5	3.5
Amphichaeta sannio	-	-	0.3	0.5	3.5	0.0	1.2	2.0	1.2	2.0
Tubifex costatus	15.3	3.3	15.0	4.7	1.2	2.0	9.3	5.4	11.7	12.3
Enchytraeidae	13.5	5.0	26.5	19.9	2.3	2.0	7.0	0.0	9.3	7.3
Hediste diversicolor	4.4	1.8	6.5	4.4	4.7	5.4	9.3	2.0	22.2	5.4
Manayunkia aestuarina	3.2	0.5	1.5	0.5	-	-	5.8	5.4	1.2	2.0
Corophium volutator	0.6	0.5	7.4	2.2	-	-	-	-	-	-
Sphaeroma hookeri	0.3	0.5	0.3	0.5	-	-	-	-	-	-
Chironomidae larve	0.3	0.5	-	-	-	-	-	-	-	-
sum	67.3	6.7	87.3	16.8	26.8	11.3	54.8	26.7	75.8	2.0

Comparison of the oligochaete abundances showed that they were scarcely affected, if at all, by enclosure in boxes or by the *H. diversicolor* density. Although increases and decreases in certain species were recorded in some experiments, these changes were not evident in other experi-

ments. In fact different experiments sometimes yielded changes in opposite directions. Experiment 4, for example, indicated that population development of *Amphichaeta sannio* inside the boxes was delayed compared with that in the open water (Table 6). However, in experiment 3 *A. sannio* was found only in the boxes (Table 5). A similar result is obtained by comparing Enchytraeidae in experiments 1 and 4 (Tables 3 and 6) with those in experiment 3 (Table 5).

Table 5 Macrofauna abundances ($\bar{x}$ = ind $\cdot$ 10 cm⁻²) in experiment 3 (see also legend of Fig. 2)

	16.05. 1990		28.05. 1990				
T a x a	O x̄	n=3 SD	I x̄	n=3 SD	BO * x̄	B1 * x̄	B2 * x̄
Hydrobiidae	36.4	7.1	27.0	7.7	31.7	43.1	36.1
Cerastoderma lamarcki	-	-	0.6	1.0	-	0.9	0.9
Paranais littoralis	2.3	0.5	6.7	3.1	3.3	-	7.9
Amphichaeta sannio	-	-	-	-	6.2	7.0	7.0
Tubifex costatus	5.6	1.8	6.8	2.7	15.0	7.0	8.8
Tubificoides benedeni	2.7	1.5	0.9	0.0	1.8	3.5	4.4
Enchytraeidae	7.3	4.5	8.5	5.4	6.2	8.8	4.4
Hediste diversicolor	7.3	3.6	9.7	3.8	6.2	8.8	12.3
Polydora ligni	-	-	0.3	0.5	-	-	-
Pygospio elegans	-	-	-	-	0.9	-	-
Streblospio shrubsolei	0.3	0.5	0.3	0.5	2.6	3.5	0.9
Heteromastus filiformis	0.3	0.5	0.3	0.5	-	-	0.9
Alkmaria romijni	2.9	1.3	1.2	0.5	-	0.9	1.8
Manayunkia aestuarina	2.6	0.9	1.9	1.3	0.9	5.3	12.3
Corophium volutator	22.6	12.7	9.1	1.4	28.2	7.9	1.8
Cyathura carinata	0.6	1.0	-	-	-	-	-
Sphaeroma hookeri	0.3	0.5	0.6	0.5	0.9	-	0.9
sum	91.5	8.9	85.1	16.4	105.6	96.8	100.4

In the second part of experiment 1, the abundance of *Paranais littoralis* decreased markedly from BO to B2 as the *H. diversicolor* density increased (Table 3). However, this tendency was not confirmed in experiments 3 and 4 (Tables 5 and 6).

The increase in *Manayunkia aestuarina* density as the density of *H. diversicolor* increased in experiment 3 is very remarkable (Tab. 5), especially since experiment 4 yielded a similar result (Table 6). Owing to the very short duration of the experiments, no conclusions regarding secondary effects resembling a three or multiple level model could be expected.

Table 6 Macrofauna abundances ($\bar{x}$ = ind · 10 cm⁻²) in experiment 4 (see also legend of Fig. 2)

T a x a	05.09.1990		20.09.1990							
	O $\bar{x}$	n = 3 SD	I $\bar{x}$	n = 3 SD	BO $\bar{x}$	n = 4 SD	B1 $\bar{x}$	n = 4 SD	B2 $\bar{x}$	n = 4 SD
Hydrobiidae	32.6	0.9	40.8	9.4	30.9	16.4	49.4	24.1	29.1	8.3
Littorina obtusata	0.3	0.5	-	-	-	-	-	-	-	-
Cerastoderma lamarcki	0.3	0.5	0.3	0.5	0.9	1.8	1.8	2.0	0.9	1.8
Paranais littoralis	5.6	1.9	5.3	0.9	7.1	2.9	7.9	5.3	8.0	7.9
Amphichaeta sannio	33.5	2.3	106.7	37.9	74.2	19.8	52.0	18.6	61.8	37.7
Tubifex costatus	9.1	2.2	7.9	4.9	0.9	1.8	7.1	4.1	7.1	5.0
Tubificoides benedeni	2.3	0.5	4.4	4.0	3.5	2.9	6.2	1.8	1.8	2.0
Enchytraeidae	5.9	2.1	4.4	6.2	0.9	1.8	2.7	3.4	0.9	1.8
Hediste diversicolor	17.0	6.6	16.5	5.7	17.7	2.9	21.2	9.1	16.5	4.6
Polydora ligni	-	-	0.6	1.0	-	-	-	-	0.9	1.8
Steblospio shrubsoi	0.6	1.0	0.9	0.0	1.8	2.0	-	-	0.9	1.8
Alkmarna romijini	0.6	1.0	11.5	13.0	0.9	1.8	2.7	5.3	-	-
Manayunkia aestuarina	6.4	6.6	8.2	3.6	4.4	5.3	12.4	11.0	9.7	6.1
Corophium volutator	6.8	0.5	10.9	6.7	8.0	3.4	3.5	0.0	2.6	1.8
Gammaridae juv.	0.6	1.0	-	-	-	-	-	-	-	-
Cyathura carinata	-	-	0.6	1.0	-	-	-	-	-	-
Idotea chelipes	-	-	-	-	-	-	-	-	0.9	1.8
Chironomidae larvae	0.3	0.5	1.2	1.3	-	-	0.9	1.8	0.9	1.8
sum	122.0	13.5	219.9	17.0	159.7	15.4	167.8	11.1	151.8	40.8

Meiozoobenthos (Table 7, Fig. 3)

The artificially increased *H. diversicolor* density did not cause generally significant changes in the overall dominance of the permanent meiofauna compared with the controls (BO). A distinct decrease was observed in only one case (B1 in part 1 of experiment 1), and in experiment 3 meiofauna colonization was much more dense at the end of the experiments in the boxes to which *H. diversicolor* had been added than in those with a natural *H. diversicolor* population density at the beginning of the experiment. The general results for meiofauna also apply in general to the nematodes since they account for the larger part of meiofauna (70 - 80 %). However, comparison of the mean values gives the impression that their abundance increased as *H. diversicolor* population density increased (exception: B1 in part 1 of experiment 1). No major changes that could be attributed to the differences in *H. diversicolor* population density were detected in the rough qualitative composition of the permanent meiofauna during the experiment. At the end of experiment 1 there was a striking increase in both copepod and nematode abundance. Although individual

densities in some boxes were significantly higher than in the surrounding open water at the end of the experiments, no definite box effect such as a compartment-induced increase in meiofauna population density could be identified.

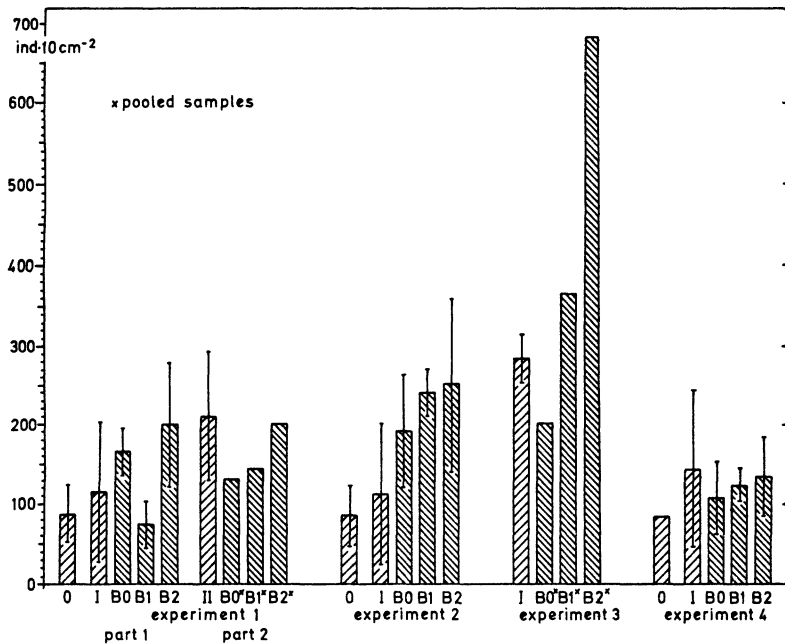


Fig. 3 Abundances ($\bar{x} \pm SD$) of the Nematoda in experiments 1 - 4
 x = pooled samples (see legend of Fig. 2)

Table 7: Abundances ($\bar{x}$ = ind $\cdot$ 10 cm⁻²; SD = standard deviation) of permanent meiofauna in experiments 1 - 4
A = experiment 1; B = experiment 2; C = experiment 3; D = experiment 4; * = pooled samples
(see also legend of Fig. 2)

Taxa	0			I			B 0			B 1			B 2			I I			B1 *			B2 *		
	$\bar{x}$	SD		$\bar{x}$	SD		$\bar{x}$	SD		$\bar{x}$	SD		$\bar{x}$	SD		$\bar{x}$	SD		$\bar{x}$	SD		$\bar{x}$	SD	
Cnidaria	A	0.2	0.5	0.3	0.6		1.0	1.7		0.8	1.5		0.8	1.5		2.3	3.2		2.4	10		18		
	B	-	-	10.3	2.1	21*	0	-		1.0	1.7		0	-										
	C	1.3	0.5	3.0	3.6	2.3	2.3	1.5		11*	9.0		33*	2.3										
	D	3.2	3.0	7.0	2.6		13.3	9.7		5.0	4.4		1.8	3.5		10.3	3.1		12	8		0		
Turbellaria	A	-	-	9.0	2.6		3.3	3.5		2.3	4.0		4.7	4.0										
	B	-	-	23.0	6.2		13*	-		9*	-		7*	-										
	C	12.0	4.6	23.0	6.2		16.5	6.0		26.0	22.3		20.0	9.6										
	D	86.8	37.9	113.7	86.7		165.0	32.5		73.5	30.3		199.0	77.8		212.0	82.9		129	144		201		
Nemertoda	A	-	-	285.0	32.1		189.0	70.9		241.0	31.2		250.0	106.7										
	B	-	-	142.7	101.5		202*	-		367*	-		682*	-										
	C	84.7	3.2	142.7	101.5		108.5	45.3		123.3	22.1		134.3	48.3										
	D	1.8	2.0	1.3	1.5		0	-		0	4.0		0.8	1.5		0			8	3		0		
Halacarida	A	-	-	0			2.3	4.0		2.3	4.0		1.0	1.7										
	B	-	-	3.3	1.5		3*	-		5*	-		11*	-										
	C	0.7	1.2	3.3	1.5		1.5	1.7		0.8	1.5		1.8	3.5										
	D	8.4	5.6	2.7	3.1		6.8	7.4		4.8	5.7		7.5	8.8		20.3	4.0		18	15		23		
Ostracoda	A	-	-	10.0	2.0		17.7	13.7		8.0	1.7		9.0	1.7										
	B	-	-	12.7	4.2		19*	-		22*	-		13*	-										
	C	8.0	6.9	12.7	4.2		10.8	2.9		14.3	5.6		5.8	6.8										
	D	6.4	4.1	6.0	6.0		24.3	3.4		4.3	3.4		7.5	5.0		31.7	10.8		96	88		66		
Copepoda	A	-	-	55.7	26.6		13.3	8.5		9.0	10.1		5.3	6.8										
	B	-	-	14.7	6.5		83*	-		77*	-		232*	-										
	C	8.0	2.0	14.7	6.5		7.5	3.3		5.0	4.4		7.5	7.6										
	D	106.8	38.5	131.0	77.0		210.4	17.9		88.4	34.7		217.4	67.7		276.6	80.0		287	268		308		
Sum	A	106.8	38.5	131.0	77.0		225.6	66.7		263.6	30.7		270.0	87.0										
	B	106.8	38.5	131.0	77.0		225.6	66.7		263.6	30.7		270.0	87.0										
	C	-	-	370.0	18.8		341*	-		491*	-		978*	-										
	D	114.7	11.4	199.4	97.5		147.1	36.0		178.4	13.5		174.4	57.3					287	268		308		

Discussion

The results of the experiments showed that a few representatives of the benthic fauna are influenced by changes in *H. diversicolor* population density. The added number of *H. diversicolor* corresponded to 0.3 (exp. 4, B1) to 4 (exp. 1, B2) times the population density outside of the boxes at the time of the experiment (Table 1). However, if we take into account that the added specimens were between 15 and 50 mm long (25 to 30 mm on average), the population density of this size class compared to that outside the boxes was raised by a factor of 8 (B1) and 16 (B2) respectively in experiments 1 and 2, 2.5 (B1) and 5 (B2) respectively, in experiment 3 and 2 (B1) and 4 (B2) respectively in experiment 4. This is important because REISE and LAMBERT (1987) showed that especially adult *H. diversicolor* exhibit territorial behaviour. This behaviour is most evident in their defense of their tube systems, but is also displayed when they seek food on the sediment surface. In our investigation area, *H. diversicolor* is uniformly distributed with territories of 2 to 4 cm². REISE (1979 a) calculated a territory size of 4 cm² for this species in the North Sea watt regions. This means that the addition of mainly adult and subadult animals with corresponding territorial requirements led to populations that were too large for the size of the boxes so that intraspecific interactions were unavoidable. This is a possible explanation for the reduced abundances of *H. diversicolor* compared with those theoretically expected in boxes B 1 and B2 in all experiments, particularly since no reduction in population density was observed in the control boxes BO, so that box effects can be precluded.

Apart from a decrease in expected population by 70 to 80 % (exp. 1), we were also able to detect a shift in length frequency. At the end of the experiment, box B2 contained only *H. diversicolor* specimens with a length of 30 mm or more ($n = 8$). Outside of the boxes, only 25 % of *H. diversicolor* belonged to this size group at the time. Similar changes in length distribution were observed in all boxes and were probably caused by two factors. Firstly, most of the animals used for our experiments belonged to this size group, and secondly the number of smaller individuals decreased substantially. However, the numbers of *H. diversicolor* with a length of 30 mm or more also decreased compared with the numbers of animals added. It is improbable that these animals escaped from the boxes through the sediment. Although ESSELINK (1989) observed that *H. diversicolor* in the length group up to 40 mm lives at an average depth of 60 mm in sandy substrates (down to 200 mm in exceptional cases), this does not apply to our experiments. We found only occasional polychaetes in tubes deeper than 60 mm.

We attribute the loss of abundance to predation pressure by larger individuals. Cannibalism has also been described for this species (GOERKE, 1971). It seems possible that the population density would decline to the optimal value for the biotope in long-term experiments.

The significant influence on *C. volutator* abundance was much more distinct than the intraspecific interaction. An increase in *H. diversicolor* abundance led in all experiments to a reduction in the population density of this amphipod (Fig. 2). COMMITO (1985) and RÖNN et al. (1988) re-

ported a similar link between Nereidae and *C. volutator* abundance. RÖNN et al. also showed that *C. volutator* reacts very sensitively to mechanical disturbances and tries to leave the area of the disturbance if possible. This may explain control value I in experiment 3, which differs markedly from the other values measured at the same point in time (Fig. 4).

In late April and early May we observed a major increase in *C. volutator* abundance from around 4,000 ind · m⁻² to between 25,000 ind · m⁻² (1990) and 55,000 ind · m⁻² (1989) within a few weeks in the investigation area (Fig. 4). The individual dominance changed from between 1 and 2 % (October to April) to around 20 % (June - August). This rapid increase in abundance was caused by reproduction. However, in June/July the abundance decreased again just as rapidly as it increased. We suspect that one of the reasons for the decrease was predation or disturbance of the juvenile *C. volutator* by *H. diversicolor*, which would thus exercise a major influence on the *C. volutator* population development. Predation on juvenile *C. volutator* caused by *H. diversicolor* larger than 20 mm was also recorded by SAMMOUR (1989) in laboratory experiments.

Fig. 4
Abundances ($\bar{x} \pm \text{SD}$) of
Corophium volutator in the
investigation area from March
1988 to November 1990

Certainly, it is difficult to prove the existence of a secondary effect on the basis of our short-term experiments. However, it is striking that in experiment 3 the density of *Manayunkia aestuarina* increased markedly as the *C. volutator* density decreased due to the higher *H. diversicolor* abundance. We found the first free-living *M. aestuarina* juveniles in mid-May during experiment 3. It seems as if the survival rate of juvenile *M. aestuarina* increases as a result of the reduced *C. volutator* density. It is not yet possible to come to a definite conclusion in this respect, but similar inferences can be drawn from experiment 4.

According to REISE (1979 b) and RÖNN et al. (1988), *H. diversicolor* does not only affect the abundance of *C. volutator*, but also that of other macrozoobenthos representatives. REISE noted that an increase in *H. diversicolor* is accompanied by a decrease in juvenile *Cerastoderma edule* (<5 mm). According to RÖNN et al., individual densities of chironomid larvae and juvenile *Macoma baltica* also decrease as the abundance of *H. diversicolor* increases. REISE also observed that the abundance of *H. diversicolor* does not correlate with the abundances of other polychaetes.

No evidence of influences on macrofauna other than the representatives mentioned here was found during our experiments. This applies to both the dominant hydrobiid snails (about 90 % *Hydrobia ventrosa*) and the oligochaetes. The other taxa were too weakly represented to permit definite conclusions. Signs of a box effect in the form of reduced abundance were observed in the case of *Amphichaeta sannio* (exp. 4) and the Enchytraeidae (exp. 1 and 4). The decrease in *Paranais littoralis* abundance observed in experiment 1 was not evident in experiments 3 and 4. The change in *H. diversicolor* population density also had no influence on the abundance of *Tubifex costatus*, a dominant species in our investigation area.

The way in which *H. diversicolor* feeds can account for the different degrees to which the various macrofauna representatives are influenced. Most oligochaete and polychaete species in our investigation area inhabit the sediment. They are therefore less exposed to direct predation by *H. diversicolor* than juvenile molluscs living on the substrate or juvenile *C. volutator* during the first phase of their migration after leaving the brood pouch of the females. *H. diversicolor* therefore has a direct effect at least on the composition and dynamics of macrobenthic epifauna.

The stocking density of *H. diversicolor* does not appear to have an appreciable influence on the abundance and rough qualitative composition of the permanent meiofauna (Table 3). The apparent slight general increase in nematode abundances (Fig. 3) accompanying the higher *H. diversicolor* density is difficult to interpret. The changes this polychaete induces in the sediment structure may provide a possible explanation. The ephemeral tubes built by this species increase the reactive surface area of the sediment, and the slime excreted during their construction suppresses resuspension and might also form a basis for a food chain that can be utilized by meiofauna. This, however, conflicts with observations made by ALONGI (1985), who reported that Protozoan individual densities and bacterial production were significantly higher in the tubes than in

the surrounding sediment, but that meiofauna was scarcely present owing to the absence of nematodes. Only the harpacticoid *Tisbe holothuriae* was found relatively frequently in the tubes. Our findings are also in contradiction to observations reported by GEE et al. (1985), GOERKE (1971) and TIETJEN (1969), who showed that *H. diversicolor* can severely decimate the permanent meiofauna, and especially nematodes.

Table 8 Statistical analysis of the results of experiments 1 and 4
* = P 0.05; ** = P 0.01; *** = P 0.001

experiment 1		experiment 4
1st part	2nd part	
0 < I**	I = II	0 = I
I = B0	II = B0	I = B0
B0 > B1**	B0 > B1***	I > B1*
B0 > B2**	B0 > B2***	I > B2*
B1 = B2	B1 = B2	B0 > B2*

Summary

The direct influence of *Hediste diversicolor* on the benthic macro- and meiofauna was investigated in four short-term experiments using submerged boxes consisting of plastic tubes with diameters of 10.5 and 19.5 cm respectively. The boxes were closed at the top with gauze (mesh size: 0.1mm) and at the bottom by the sediment surface. They were loaded with different numbers of *H. diversicolor*, one remaining untreated as control. A definite influence of *H. diversicolor* was only recorded for the amphipod *Corophium volutator*, which was negatively affected by artificially increased individual numbers of this polychaet. The infaunal polychaete and oligochaete showed no significant response to the higher *H. diversicolor* density. Although there were signs of a slight increase in nematode abundances accompanying the higher *H. diversicolor* density, the stocking density of this polychaet does not appear to have an appreciable influence on the abundance and rough qualitative composition of the permanent meiofauna.

Zusammenfassung

Um den direkten Einfluß von *Hediste diversicolor* auf die Makro- und Meiofauna zu überprüfen, wurden in einem Flachwassergebiet der Mecklenburger Bucht Kurzzeit-Boxexperimente durchgeführt. Künstlich erhöhte Individuendichten dieses Polychaeten in den Boxen hatten Verringerungen der Abundanzen von *Corophium volutator* zur Folge. Vermutlich wird die natürliche Population von *C. volutator* in diesem Gebiet in ähnlicher Weise beeinflusst.

Die Abundanzen der Oligochaeten- und Polychaetenarten veränderten sich nicht signifikant. Innerhalb der permanenten Meiofauna erhöhte sich die Individuendichte der Nematoden leicht. Eine deutliche Abnahme der *Hediste diversicolor*-Abundanzen in den Versuchsboxen deutet auf intraspezifische Wechselwirkungen durch Kannibalismus oder Konkurrenz um Raum oder Nahrung hin.

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