

## The diet of *Enoplus brevis* (Nematoda) in a supralittoral salt marsh of the North Sea

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**ABSTRACT:** The gut content of nearly 2000 specimens of *Enoplus brevis* was quantitatively analysed. *E. brevis* is an opportunistic omnivore. Main food categories found were cyanobacteria, diatoms, oligochaetes, nematodes, and rotifers. With a few exceptions, the diet of females and males was identical. Predominantly, juveniles fed on cyanobacteria and adults on animal prey. Experiments revealed that living oligochaetes are attacked and preyed upon. The quantities of the food categories eaten by *Enoplus* varied according to their ambient abundance, both temporarily and spatially on a small scale. At least the nematode prey was strongly selected: some species were significantly preferred and others avoided.

### INTRODUCTION

Nematodes are a major component of meiofaunal assemblages all over the world. In fine grained marine and brackish sediments they are usually the numerically dominant taxon (Heip et al., 1982, 1985). This is also true for the supralittoral salt marshes of the North Sea (Armonies, 1986b) where nematodes compete with plathelminths for the highest species richness (Lorenzen, 1969; Hellwig, 1986; Armonies, 1986b). In the investigated salt marsh, *Enoplus brevis* Bastian, 1865 is one of the largest and most abundant meiofaunal species. Therefore, it is suspected to be a key-species of the aquatic meiofaunal food-web in these salt marshes.

Information on food and feeding in free-living marine nematodes is scarce and mainly limited to species cultured on bacteria, yeasts, and algae (reviewed by Tietjen & Lee, 1977; Heip et al., 1985; Jensen, 1987). In this study, the trophic position of *E. brevis* is evaluated by comparing the qualitative and quantitative composition of the organisms ingested by *Enoplus* specimens freshly collected in the field and of the organisms occurring in the same salt marsh habitats.

## MATERIAL AND METHODS

### Sample sites

Samples were collected from a supralittoral salt marsh in the northernmost part of the island of Sylt in the northern Wadden Sea (German Bight). The marsh is intensively grazed by sheep which keep the vegetation short (1.5 to 3 cm) and poor in species. The lower part of the salt marsh is covered by the plant association *Puccinellion maritimae* and the upper part by an *Armerietum maritimae* (cf. Ellenberg, 1982; Dijkema, 1983). The dominant plant species in the lower marsh are the grass *Puccinellia maritima* (Huds.) and *Salicornia* species while the juncacean *Juncus gerardii* Lois. and the poacean *Festuca rubra* (L.) dominate in the upper marsh.

The height of the salt marsh sediment ranges from 15 to 120 cm above mean high tide level. The combined effects of seawater flooding, groundwater pressure, precipitation, and evaporation cause strong salinity variations, temporarily as well as spatially on a small scale. Samples were collected in August 18, 1988 and January 12, 1989 at 10 locations spread over the entire salt marsh. Within the lower marsh, salinity varied between 20 and 60‰ in August. In January it was less variable (23 to 28‰). At both dates, salinity of the upper marsh was lower and more stable (3 to 15‰). This salinity pattern with high fluctuations in the lower and moderate variations in the upper part seems to be typical of boreal salt marshes (Bilio, 1964; Armonies, 1986a). The sediment is muddy with a very high proportion of plant material (20 to 40 % of dry weight; Armonies, 1986b).

### Sampling and extraction

At both sampling dates, two samples of 5 cm<sup>2</sup> surface area and 4 cm depth were collected at 5 stations following the difference in elevation of the sediment surface in steps of 25 cm. At each station, one sample was taken from a slightly elevated and another from a slightly depressed site. Because of the dense rootage, samples were cut off with a knife.

Meiofauna was extracted from the samples using the procedure described by Armonies & Hellwig (1986). Samples are fitted into glass tubes and covered with a layer of clean coarse sand. The sand is moistened with water of ambient salinity and the sample stored in the dark. Animals inside the sediment are expected to follow the increasing gradient of oxygen and, therefore, to move upward into the sandy layer. This sand is separated periodically until all of the sample turns black. A shaking-decantation procedure was used to remove the fauna from the sand. Since this method is not 100 % effective for nematodes from supralittoral salt marshes, a fifth of the sediment was pulled to pieces after extraction, and sorted for non-extracted specimens.

All metazoans were determined to higher taxa and counted. *Enoplus brevis* was separated, transferred to slides, and enclosed in a drop of polyvinyl-lactophenol. This fixative clears up the dark brown pigments around the intestine and thus allows microscopic inspection of its contents. All other nematodes were preserved in 5% formalin for later identification.

### Feeding experiment

Inspections of the intestine can only show the variety and composition of the diet. However, the occurrence of animal remains such as oligochaete setae cannot indicate whether *Enoplus* is a predator or a scavenger. Therefore, feeding experiments were conducted. Five mature *Enoplus brevis* and 5 *Lumbricillus enteromorphae* v. Bülow, 1957 (Oligochaeta) were enclosed in 5-cm<sup>3</sup> glass tubes with a small amount of coarse sand. In previous choice experiments for grain sizes (cafeteria design), *Enoplus* preferred sand with a median diameter of 0.25 mm or more. Glass tubes containing 5 oligochaetes and coarse sand but without *Enoplus* served as controls. The experiment and controls were replicated 10-times. This experiment was run once using large oligochaetes (at least twice the length of *Enoplus*) and once with small oligochaetes of about the same length as *Enoplus*. A U-test (Sachs, 1984) was used to test for a significant decrease in the number of oligochaetes in the presence of *E. brevis*.

### Statistical analyses of the intestine contents

The intestinal contents of every single specimen may be regarded as a replicate sample. However, a priori it was suspected that (a) many food items cannot be properly quantified, and (b) the numerical abundances of various food categories in a single *Enoplus* are not independent of each other. In case (a), some food can only be quantified indirectly. For example, the number of oligochaete setae found in the intestine of *Enoplus* is treated as an indicator of the amount of ingested oligochaete tissue. In case (b), high abundance of one food item, say diatoms, leaves little free intestinal space and thus restricts the probability of the occurrence of other food items. For statistical analyses of the intestinal contents, all *Enoplus brevis* from a single sample are pooled, and the distribution of food items among all specimens of the sample is compared to that of other sample sites.

Because of the difficulties in quantifying some food numerically, the occurrence of every food item was transferred to categories of abundance, e.g. no cyanobacteria, few (up to about 25% of the intestinal space), and many (> 25%) cyanobacteria in one *Enoplus*. These categories of abundance are statistically compared to other categories like seasons, wet and dry places in the marsh, or the upper and lower parts of the salt marsh. Differences in the distribution of data in such a two-way categorial matrix are properly analysed by  $\chi^2$  tests of homogeneity in a contingency table (Sachs, 1984). However, since the abundances of various food items may not be independent of each other (see above) and because the same data are used for several comparisons, only test results with a probability level  $p < 0.01$  (indicated by \*\*) are treated as significant, although results with  $0.05 > p > 0.01$  are also indicated (by \*).

## RESULTS

In both seasons and at each station, nematodes were the most abundant metazoans, followed by Copepoda and Oligochaeta (Table 1). Abundance was generally lower in summer than in winter. In summer *Enoplus brevis* accounted for 1221 of a total of 13 150 nematodes found (9.3%), in winter for 1331 of a total of 22 028 (6.0%) in the lower marsh,

Table 1. Metazoan meiofauna of the studied salt marsh in summer, winter, and mean of seasons. Individuals per 10 cm<sup>2</sup> (standard deviation in brackets)

Taxon		Puccinellietum (Lower marsh)	Armerietum (Upper marsh)	Entire marsh
Nematoda	Summer	3600 (312)	1174 (726)	2630 (1396)
	Winter	7343 (2459)	5265 (769)	6512 (2113)
	Mean	5472	3220	4571
Copepoda	Summer	176 (35)	268 (244)	213 (134)
	Winter	305 (214)	311 (160)	308 (171)
	Mean	241	290	261
Oligochaeta	Summer	154 (38)	124 (26)	142 (34)
	Winter	187 (85)	201 (94)	192 (77)
	Mean	171	163	167
Plathelminthes	Summer	29 (37)	34 (9)	31 (27)
	Winter	47 (25)	66 (24)	54 (24)
	Mean	38	50	43
Rotatoria	Summer	0	48 (32)	19 (31)
	Winter	59 (80)	140 (14)	91 (72)
	Mean	30	94	55
Halacaridae	Summer	18 (10)	10 (6)	15 (9)
	Winter	12 (14)	35 (18)	21 (18)
	Mean	15	23	18
Insect-larvae	Summer	4 (2)	8 (7)	6 (4)
	Winter	13 (8)	18 (3)	15 (6)
	Mean	9	13	11
Total	Summer	3981	1666	3056
	Winter	7966	6036	7194
	Mean	5974	3851	5125

and for 195 of 10 530 (1.9 %) in the upper marsh. This equals an average abundance of 224 per 10 cm<sup>2</sup> in summer and 305 in winter. The intestinal contents of 751 (summer) and 1140 (winter) specimens were inspected.

#### Summer diet

The following food items were found in the intestine: cyanobacteria (*Microcoleus/Oscillatoria* formation, cf. Polderman, 1979, p. 127), pennate diatoms, nematodes and remainders of the latter (spicula, hardened structures of the buccal cavity), rotifers (or their mastax), oligochaete setae, and only once remainders of a copepod. In addition unidentified plant material was observed, further on called detritus. Cyanobacteria and diatoms lose their colour while passing through the intestine, and the intestinal contents take on a greenish to yellowish colour in the caudal part of the worms. This indicates that diatoms and cyanobacteria are digested at least in part.

The qualitative and quantitative composition of food items did not differ between adult males and females. However, the diet changed with increasing body size. Juveniles

consumed significantly more cyanobacteria than adults (Table 2). In fact, bluegreen algae were even the most important food of juvenile *Enoplus*. At sample sites with few cyanobacterians, the intestine of juveniles often contained only detritus or a few diatoms or was even empty. The numbers of diatoms, nematodes, rotifers, and oligochaete setae in the intestines increased significantly with increasing body size (Table 2).

Table 2. Summer diet of *Enoplus brevis*. Numbers and percentages of specimens which had the respective food item in their intestinal cavity. The  $\chi^2$  tests for differences between juveniles and adults.  $\chi^2$  tests using size classes of *Enoplus* instead of the maturity categories yielded similar results

Food		Total	Juveniles	Adults	$\chi^2$ test	Df
Cyanobacteria	many	64 (9 %)	57 (17 %)	7 (2 %)	56.2***	2
	few	226 (30 %)	91 (27 %)	135 (33 %)		
	none	453 (61 %)	183 (55 %)	270 (66 %)		
Diatoms	> 10	151 (20 %)	35 (11 %)	116 (28 %)	48.1***	2
	1-9	351 (47 %)	154 (47 %)	197 (48 %)		
	none	241 (32 %)	142 (43 %)	99 (24 %)		
Oligochaete setae	> 15	87 (12 %)	3 (1 %)	84 (20 %)	168.9***	3
	6-15	159 (21 %)	30 (9 %)	129 (31 %)		
	1-5	186 (25 %)	88 (27 %)	98 (24 %)		
	none	311 (42 %)	210 (64 %)	101 (25 %)		
Nematodes	1 or more	138 (19 %)	37 (11 %)	101 (25 %)	21.6***	1
	none	605 (81 %)	294 (89 %)	311 (75 %)		
Rotatoria	1 or more	26 (3 %)	5 (2 %)	21 (5 %)	7.0**	1
	none	724 (97 %)	330 (98 %)	394 (95 %)		
Detritus	only	44 (7 %)	36 (12 %)	8 (2 %)	29.2***	1
	also other food	631 (93 %)	253 (88 %)	378 (98 %)		
Intestine	empty	75 (9 %)	46 (14 %)	29 (7 %)	9.3**	1
	not empty	675 (91 %)	289 (86 %)	386 (93 %)		

### Winter diet

In winter the same food items were observed in the guts of *E. brevis* as in summer. In addition, remainders of a few turbellarians were identified. In accordance with the summer samples, juveniles ingested more cyanobacteria and detritus than adults whereas the latter ingested more diatoms, oligochaetes, and rotifers than did juveniles (Table 3). In contrast to the summer results, there were some differences in the winter diet of females and males. Females consumed more diatoms (Fig. 1;  $\chi^2 = 11.94$ , df = 5,  $p < 0.05$ ) and nematodes ( $\chi^2 = 4.12$ , df = 1,  $p < 0.05$ ) than males.

### Temporal variation of the diet

The quantitative composition of the food showed strong seasonal variability. Juveniles ate significantly more cyanobacteria in summer than in winter (Fig. 2) while both adults and juveniles consumed significantly more diatoms in winter than in summer

Table 3. Winter diet of *Enoplus brevis*. Numbers and percentages of specimens which had the respective food item in their intestinal cavity. The  $\chi^2$  tests for differences between juveniles and adults

Food		Total	Juveniles	Adults	$\chi^2$ test	Df
Cyanobacteria	many	22 (4 %)	16 (5 %)	6 (2 %)	6.9*	2
	few	162 (28 %)	96 (30 %)	66 (24 %)		
	none	404 (69 %)	204 (65 %)	200 (74 %)		
Diatoms	> 100	8 (1 %)	3 (1 %)	5 (2 %)	38.2***	5
	61-100	26 (4 %)	9 (3 %)	17 (6 %)		
	31-60	80 (14 %)	28 (9 %)	52 (19 %)		
	11-30	130 (22 %)	58 (18 %)	72 (27 %)		
	1-10	218 (37 %)	129 (41 %)	89 (33 %)		
	none	125 (21 %)	89 (28 %)	36 (13 %)		
Oligochaete setae	> 15	22 (4 %)	2 (1 %)	20 (7 %)	67.3***	3
	6-15	78 (13 %)	17 (5 %)	61 (23 %)		
	1-5	116 (20 %)	58 (18 %)	58 (21 %)		
	none	371 (63 %)	239 (76 %)	132 (49 %)		
Nematodes	1 or more	124 (21 %)	59 (19 %)	65 (24 %)	2.4 ns	1
	none	463 (79 %)	257 (81 %)	206 (76 %)		
Rotatoria	> 3	11 (2 %)	0 (0 %)	11 (4 %)	18.7***	3
	2-3	39 (7 %)	15 (5 %)	24 (9 %)		
	1	51 (9 %)	25 (8 %)	26 (10 %)		
	none	486 (83 %)	276 (87 %)	210 (77 %)		
Detritus	only	53 (9 %)	40 (13 %)	13 (5 %)	11.6***	1
	and other food	515 (91 %)	262 (87 %)	253 (95 %)		
Intestine	empty	19 (3 %)	14 (4 %)	5 (2 %)	3.1 ns	1
	not empty	568 (97 %)	302 (96 %)	266 (98 %)		

(Figs 2, 3). The percentages of *Enoplus* with either oligochaete setae in the intestine or with an empty intestine were both higher in summer than in winter. The winter diet contained a higher amount of rotifers and (only in juveniles) of nematodes than the summer diet (Fig. 2). This coincides with the generally higher abundance of rotifers and nematodes in winter.

#### Comparison of the diet in the lower and upper marsh

In summer, *Enoplus* specimens from the lower marsh had significantly more cyanobacteria, diatoms, nematodes, and oligochaete setae in their intestines than specimens from the upper salt marsh. The number of animals with an empty intestine was 4-fold higher in the upper marsh (Fig. 4). In winter, the diet of specimens from both parts of the marsh displayed less differences. Nevertheless, specimens from the lower marsh consumed more oligochaetes while those from the upper marsh ate more rotifers (Fig. 4). In both prey taxa, the abundance in the sediment correlates positively with the number eaten by *Enoplus* (Spearman rank correlation coefficient, Oligochaeta  $r = +0.976$ ,  $p < 0.001$ ; Rotatoria  $r = +0.631$ ,  $p < 0.05$ ).

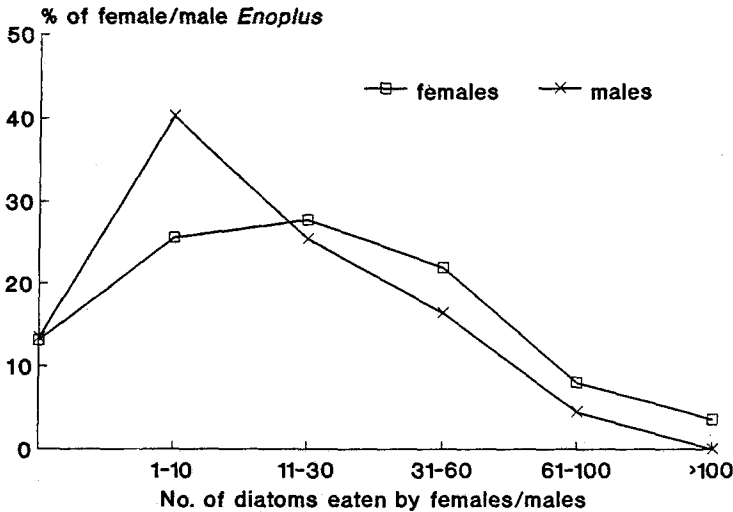


Fig. 1. Differential feeding of female and male *Enoplus* on diatoms in winter. More than 50% of males consumed 10 diatoms or less while > 60% of females consumed > 10 diatoms

#### Small-scale spatial variability of the diet

Cyanobacteria and diatoms occur more frequently at the slightly elevated sites than in the wet depressions throughout the year, while nematodes and oligochaetes are more abundant in the depressions than on elevated ground during summertime. These differences are well reflected in the abundance of food items in the *Enoplus* specimens from the respective sites (Fig. 5). Animals with an empty intestine were always more numerous in depressions.

#### Selection of the nematode food

The nematode fauna ingested by *Enoplus* specimens differed significantly from that found in the sediment inhabited by *Enoplus*. Especially *Microlaimus globiceps*, *Chromaspirina thieryi*, *Haliplectus dorsalis*, and *Theristus* species were avoided, whereas *Anoplostoma viviparum*, *Syringolaimus striaticaudatus*, *Chromadora nudicapitata*, *Tripyloides marinus*, and various species of the taxon Tylenchida were preferred as food (Table 4). Because of higher densities, the differences of abundance outlined were more obvious in winter.

#### Influence of extraction on the intestine contents

The used method of extraction depends on active vertical migrations of the animals into the added upper layer of sand. As the samples are stored at field temperature, extraction is faster in summer than in winter. In summer, high numbers of *Enoplus* invaded the sandy cover within two days. Only these specimens were used for examining the intestinal content. In winter, only a small portion of *Enoplus* had left the sediment during the same time. These latter specimens (termed E-I in the following) and those

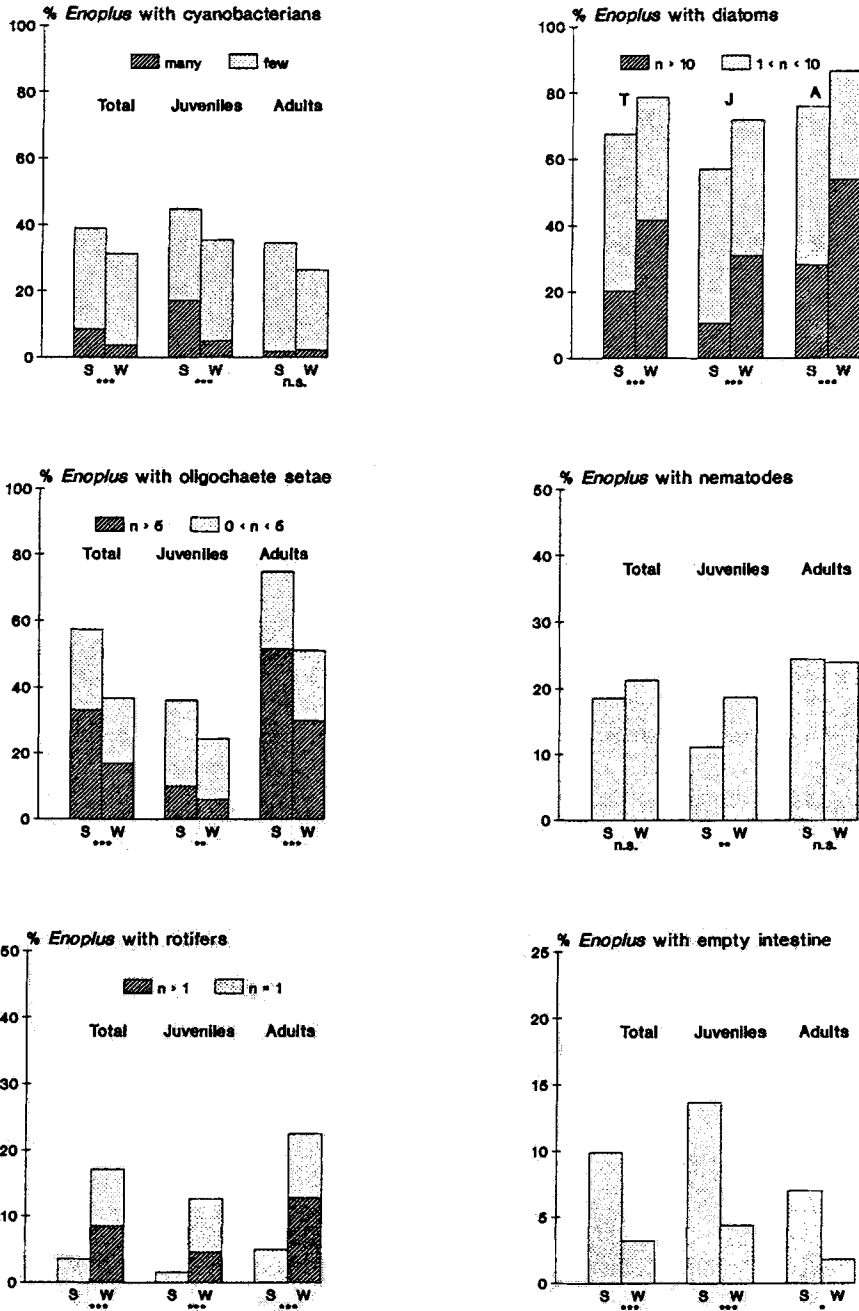


Fig. 2. Abundance of food items in the intestine of *Enoplus* in summer (S) and winter (W). The results of  $\chi^2$  tests for differences between seasons are indicated by \* ( $p < 0.05$ ), \*\* ( $p < 0.01$ ), and \*\*\* ( $p < 0.001$ ); n.s. not significant. Different shading of the columns refer to abundance classes of the food in *Enoplus*



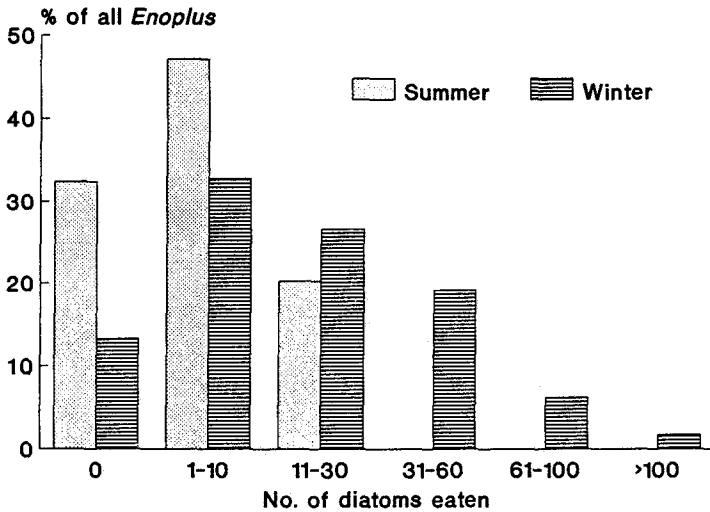


Fig. 3. Consumption of diatoms in summer and winter. High abundance of ingested diatoms was only found in winter ( $\chi^2 = 167.4$ ,  $df = 5$ ,  $p < 0.001$ )

extracted after additional two days from the same samples (E-II) were used in the above evaluation. Animals which left the sediment later (E-III) were treated separately to test the potential influence of extraction.

E-I and E-II *Enoplus* specimens do not differ significantly with respect to their animal diet ( $p > 0.05$ ). However, E-I specimens consumed more cyanobacteria and diatoms than E-II specimens (Fig. 6). The gut content of E-III specimens differed largely from that of E-I and E-II specimens: The former consumed significantly less cyanobacteria, diatoms, nematodes, oligochaetes, and rotifers but more detritus (Fig. 6). In addition, more E-III *Enoplus* had an empty intestine but most of them were very small, presumably recently hatched. In no case had E-III animals fed on food items not found in E-I and E-II specimens. Thus, extraction did not alter the food quality. The course or efficiency of extraction of a nematode species did in no case correlate with the percentage consumed by *Enoplus brevis*.

#### Predation on living oligochaetes

Both control and experimental glass jars were microscopically inspected after 3, 7, and 14 days, and surviving *Enoplus brevis* and *Lumbricillus enteromorphae* were counted. The number of *L. enteromorphae* was significantly reduced in jars containing *Enoplus* whereas the number was not reduced in jars without *Enoplus* (Fig. 7). Oligochaetes in the same size class as the tested *Enoplus* (about 5 mm) were rapidly attacked and eaten. But *Enoplus* consumed only 3 of a total of 50 mature *Lumbricillus* (of about twice the length of *Enoplus*).

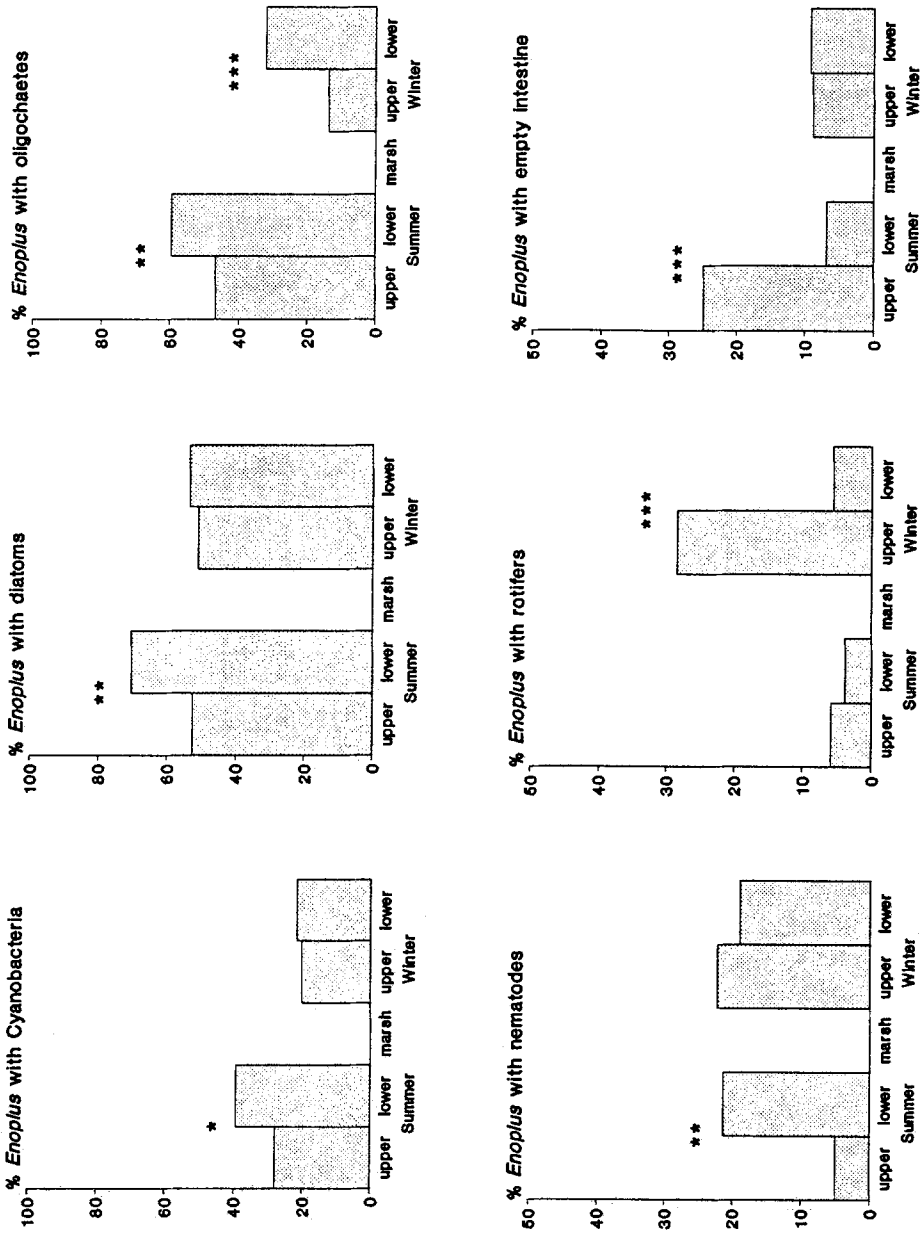


Fig. 4. Occurrence of food items in the gut of *Enoplosus brevis* from the upper (*Armerietum*) and lower (*Puccinellietum*) salt marsh. Asterisks indicate the results of  $\chi^2$  tests for a significant difference between marsh levels (df = 1)

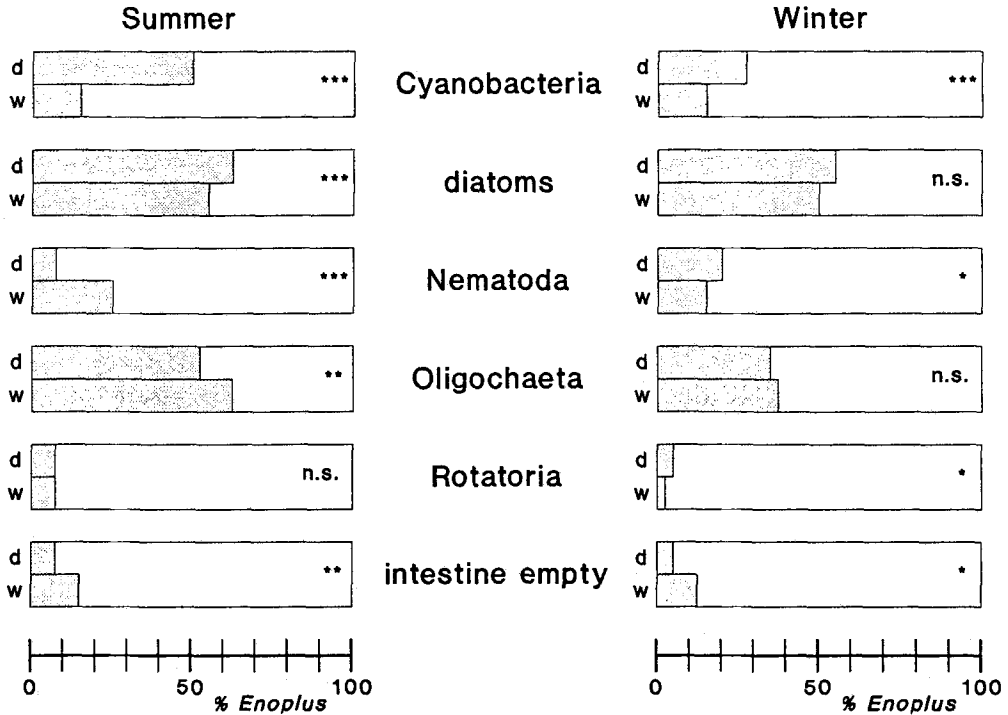


Fig. 5. Percentage occurrence of food items in *Enoplus* from small-scale elevations (d, dry) and depressions (w, wet) of the salt marsh surface. Asterisks indicate a significant spatial difference in the abundance of food items in the gut of *E. brevis* ( $\chi^2$  test,  $df = 1$ )

DISCUSSION

Reliability of gut content analyses

In the investigated salt marsh the most abundant food items in the gut of *Enoplus brevis* were diatoms (occurring in 72.4% of all specimens), oligochaetes (48.7%), cyanobacteria (35.6%), nematodes (19.7%), and rotifers (9.5%). Only a few turbellarians and copepods were consumed although these animals were fairly abundant (Table 1). Copepods possibly cannot be caught and the few turbellarians all belonged to species capable of encystment (cf. Armonies, 1986c). Presumably, only the immobile cysts were ingested. On the other hand, only prey items with hardened, more indigestible structures such as rotatorian mastax, oligochaete setae, and carcasses of swallowed crustaceans can be recognized in the gut. Therefore, juvenile turbellarians as well as microorganisms possibly ingested may have escaped our attention.

Juveniles and females of some nematode species provided with weak buccal structures may similarly have been partly overlooked. This may have biased the significantly lower percentages of such species in the gut of *Enoplus* as compared to those of the ambient sediment (*Theristus* species, *Chromaspirina thieryi*, and *Haliplectus dorsalis* in

Table 4. Nematode prey selection of *Enoplus brevis* in the lower marsh in winter. Comparison of nematode abundances in the intestine of *Enoplus* (N = 145) and the ambient sediment (N = 21 993). The  $\chi^2$  tests the null-hypothesis of equal percentages in the sediment and intestine, i.e. no prey preference or rejection. For all tests  $df = 1$ . + and - indicate a significant preference for, respectively, avoidance of a nematode species; ns, not significant

Nematode species	Abundance in <i>Enoplus</i>	Ambient abundance	$\chi^2$ test
<i>Enoplus brevis</i>	5 (3.4 %)	1331 (6.1 %)	2.06 ns
<i>Microlaimus globiceps</i>	1 (0.7 %)	3516 (16.0 %)	26.68*** -
<i>Anoplostoma viviparum</i>	40 (27.6 %)	2073 (9.4 %)	49.36*** +
<i>Chromaspirina thieryi</i>	0	1964 (8.9 %)	14.96*** -
<i>Theristus</i> (6 species)	2 (1.4 %)	3143 (14.3 %)	20.97*** -
<i>Diplolaimelloides oschei</i>	7 (4.8 %)	1607 (7.3 %)	1.66 ns
<i>Haliplectus dorsalis</i>	0	1175 (5.3 %)	8.61** -
Dorylaimida	12 (8.3 %)	1039 (4.7 %)	3.29 ns
<i>Chromadorina supralitoralis</i>	4 (2.8 %)	749 (3.4 %)	0.28 ns
<i>Syringolaimus striaticaudatus</i>	18 (12.4 %)	732 (3.3 %)	33.14*** +
<i>Innocuonema tentabundum</i>	2 (1.4 %)	636 (2.9 %)	1.35 ns
<i>Chromadora nudicapitata</i>	11 (7.6 %)	547 (2.5 %)	13.72*** +
Tylenchida	9 (6.2 %)	303 (1.4 %)	22.25*** +
<i>Dichromadora scandula</i>	0	308 (1.4 %)	2.16 ns
<i>Microlaimus honestus</i>	2 (1.4 %)	277 (1.3 %)	0.01 ns
<i>Desmolaimus bulbulus</i>	0	256 (1.2 %)	0.18 ns
<i>Camacolaimus tardus</i>	0	236 (1.1 %)	1.65 ns
<i>Sphaerolaimus gracilis</i>	2 (1.4 %)	184 (0.8 %)	0.40 ns
<i>Dolicholaimus marioni</i>	3 (2.1 %)	159 (0.7 %)	3.21 ns
<i>Deontolaimus papillatus</i>	0	142 (0.6 %)	0.94 ns
<i>Diplolaimelloides islandicus</i>	0	136 (0.6 %)	0.90 ns
<i>Tripyloides marinus</i>	5 (3.4 %)	60 (0.3 %)	46.66*** +
Tylenchida gen. spec.	11 (7.6 %)	8 (>0.1 %)	476.15*** +
Other species	10	1412	

Table 4). In very abundant species, a similar bias can be eliminated by only considering males (which can be identified by their spicula). For instance, the males of *Microlaimus globiceps* are significantly avoided by *Enoplus* as is the case for all *M. globiceps*. Three of the nematode species (in Table 4) rarely or never eaten attain a brown colour after formalin fixation. It may be speculated that this refers to a common chemical property of the cuticula which protects these species from predation by *Enoplus*.

Some of the nematode species which were significantly preferred by *Enoplus* have conspicuously hardened buccal structures (*Anoplostoma viviparum* and *Syringolaimus striaticaudatus* in Table 4); their abundance observed in the gut of *Enoplus* will equal the real abundance of specimens consumed. In *S. striaticaudatus*, even halves of eaten animals can be determined by their special tail structures. The percentages of preferentially eaten species without conspicuous buccal structures (which were mainly identified by the spicula) may be underestimated (*Chromadora nudicapitata* and *Tripyloides marinus* in Table 4).

The differences in the diet of *Enoplus* which left the sediment during the first days of extraction (E-I and E-II) and those extracted later (E-III) may be interpreted as a reaction

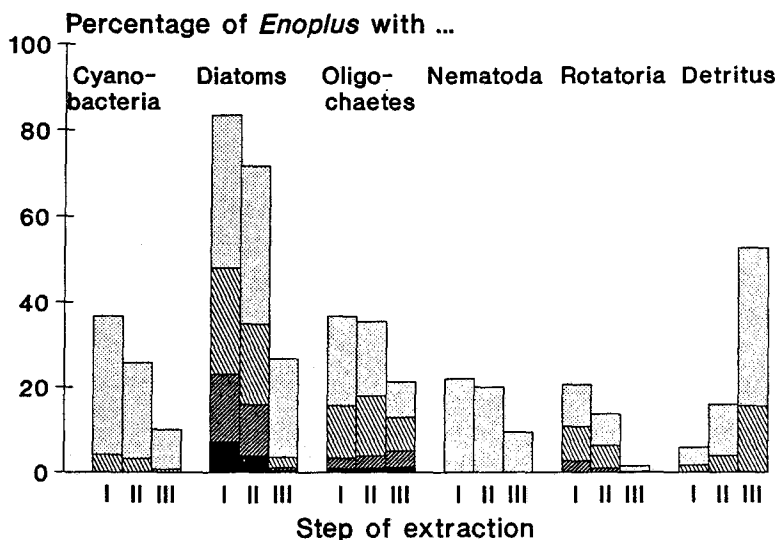


Fig. 6. Percentage occurrence of food items in *Enoplus* extracted during the first (I), second (II), and third (III) period of incubation.  $\chi^2$  tests for differences of food abundance over the entire extraction period are in all cases highly significant ( $p < 0.001$ ). Different shading of the column segments refers to different abundance classes of the food according to Table 3

to the changes of food abundance during extraction. All major food taxa including cyanobacteria and diatoms invade the added sandy cover faster than most nematodes, and extraction is rather quantitative. Depletion of food results. Specimens of *Enoplus* which left the sediment first were presumably those which stayed closest to the sediment surface where diatoms and cyanobacteria attain highest abundance. The higher proportion of specimens which fed on these items may therefore be explained as density-dependent food consumption. The high numbers of specimens with an empty gut may be a result of decreasing oxygen levels which may have hampered feeding. Finally, gut passage time of the food items may differ which may also contribute to the different diet of E-III *Enoplus*.

The feeding experiment demonstrated that both living and dead oligochaetes are consumed. Oligochaetes in the same size range as *Enoplus* were preferred to larger ones. However, the gut often contained even some setae of *Enchytraeus albidus* Henle, 1837 (8 to 35 mm long), although it is unknown if they were eaten dead or alive. *Paranais litoralis* (Müller, 1784) was another oligochaete often consumed. From the shape and sizes of the swallowed setae it seems that all oligochaete species are preyed upon.

#### Position of *Enoplus brevis* in the salt marsh food web

According to the composition of the diet of vegetable and animal food, *Enoplus brevis* can be regarded as omnivorous. Juveniles preferred cyanobacteria, and adults consumed more oligochaetes and nematodes (Tables 2, 3). The percentage contribution of the food categories varied both seasonally and spatially within the marsh according to

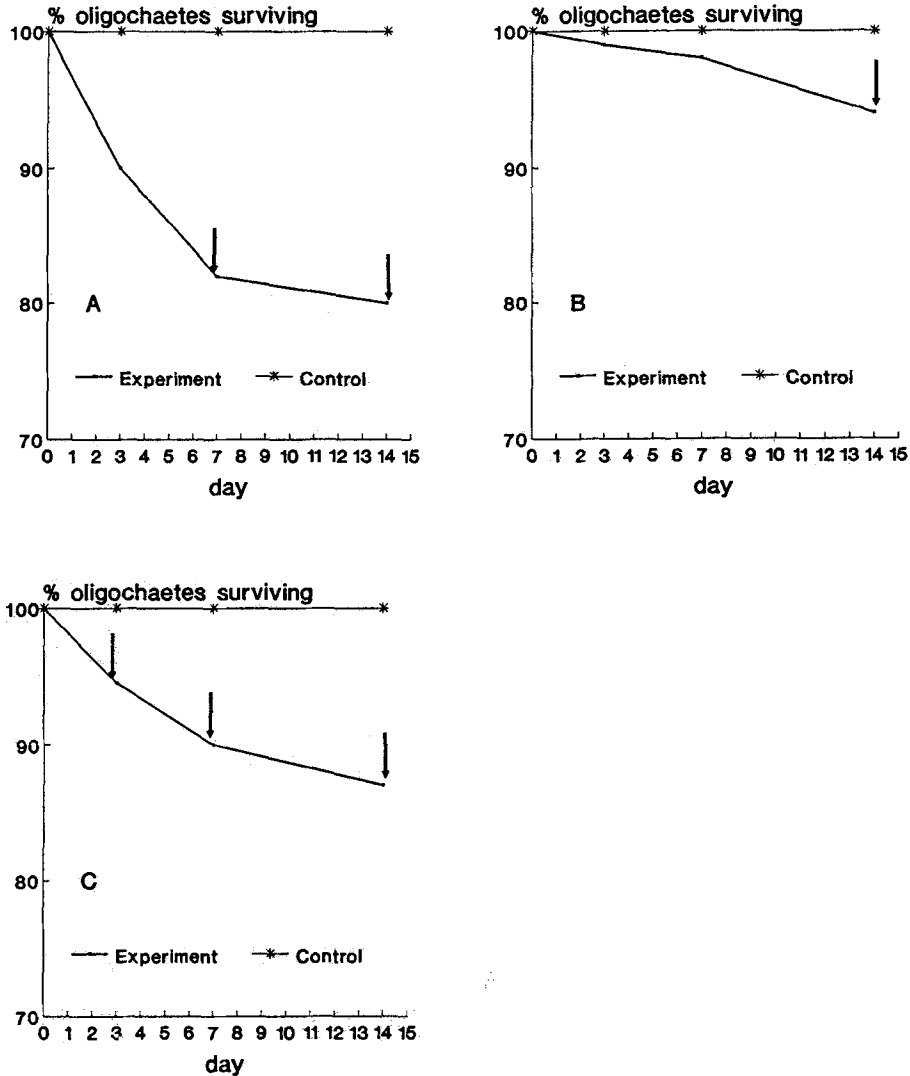


Fig. 7. Survival of oligochaetes in the presence of *Enoplus brevis* (Experiment) and without *Enoplus* (Control). Arrows indicate a significant decrease of oligochaete survival in treatments with *Enoplus* (U-test,  $p < 0.05$ ). A: small oligochaetes; B: large oligochaetes; C: both combined

the abundance of food items. Thus, *Enoplus* has an opportunistic feeding strategy. Presumably, this is the only way for such a large species to survive in high density in these salt marshes. On the other hand, some nematode species are preferred as food while other nematode species, turbellarians, and copepods are avoided. With regard to the latter, *Enoplus* may be incapable of catching them (copepods), of finding them (very small nematodes), or they are dangerous such as the *Enoplus*-eating turbellarian *Proxenetes deltoides* Den Hartog, 1965.

According to its buccal cavity structure, *E. brevis* was classified as an omnivore-predator by Wieser (1953) and as a predator by Jensen (1987). Heip et al. (1985) have pointed out the disadvantages of such schematic classification. Up to now, only little information is available on the feeding behaviour of species of the order Enoplida. Even this sparse information indicates that species of this taxon may change their feeding habits during growth; this has been observed in the Oncholaimidae *Oncholaimus oxyuris* and *Adoncholaimus thalassophygas* (Heip et al., 1985; Lopez et al., 1979). Our findings on the diet of *Enoplus brevis* fit well with the latter. Although the buccal cavity of *E. brevis* alters moderately, at the most, during postembryonic development, the spectrum of ingested food changes considerably. Thus, the armature of the buccal cavity can indicate, at the most, some mechanical ability of handling prey rather than the food preferred.

These results demonstrate the value of quantitative field studies. Laboratory cultures can only offer a restricted range of food species and are therefore unable to reveal the ecological significance of the various food categories. It is suggested that a quantitative study of the food in the field be carried out first, in order to be able subsequently to offer a realistic spectrum of prey in laboratory cultures for further investigations.

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