ORIGINAL ARTICLE

Meiofauna as food source for small-sized demersal fish in the southern North Sea

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Abstract Meiofauna play an essential role in the diet of small and juvenile fish. However, it is less well documented which meiofaunal prey groups in the sediment are eaten by fish. Trophic relationships between five demersal fish species (solenette, goby, scaldfish, dab <20 cm and plaice <20 cm) and meiofaunal prey were investigated by means of comparing sediment samples and fish stomach contents collected seasonally between January 2009 and January 2010 in the German Bight. In all seasons, meiofauna in the sediment was numerically dominated by nematodes, whereas harpacticoids dominated in terms of occurrence and biomass. Between autumn and spring, the harpacticoid community was characterized by *Pseudobradya minor* and *Halectinosoma canaliculatum*, and in summer by *Longipedia coronata*. Meiofaunal prey dominated the diets of solenette and gobies in all seasons, occurred only seasonally in the diet of scaldfish and dab, and was completely absent in the diet of plaice. For all fish species (excluding plaice) and in each season, harpacticoids were the most important meiofauna prey group in terms of occurrence, abundance and biomass. High values of Ivlev's index of selectivity for *Pseudobradya* spp. in winter and *Longipedia* spp. in summer provided evidence that predation on harpacticoids was species-selective, even though both harpacticoids co-occurred in high densities in the sediments. Most surficial feeding strategies of the studied fish species and emergent behaviours of *Pseudobradya* spp. and *Longipedia* spp. might have caused this prey selection. With increasing fish sizes, harpacticoid prey densities decreased in the fish stomachs, indicating a diet change towards larger benthic prey during the ontogeny of all fish species investigated.

Keywords Meiofauna · Flatfish · Gobiids · Harpacticoids · Prey selection

Communicated by Heinz-Dieter Franke.

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Introduction

The crucial importance of meiofauna (by definition animals passing through a 0.5-mm or 1.0-mm mesh sieve, but retained on a 63-µm mesh, Gee 1989) as food for higher trophic levels in marine food webs has been extensively investigated (e.g. Sogard 1984; Fitzhugh and Fleeger 1985; Tipton and Bell 1988; Nelson and Coull 1989; Coull et al. 1995). Many fish species, such as flatfish and gobies, feed

on meiofaunal species such as harpacticoid copepods, making this prey group an essential factor governing fish survival and growth, especially of the juvenile stages. Yet, insights into the functional details of this predator–prey relationship remain to be explored, including, for example, feeding behaviour and predation impacts on the meiofauna community in the sediments.

Meiofauna communities consist of a great diversity of species, with only a few numerically dominant groups, foremost nematodes and harpacticoid copepods (Gee 1989). Nematodes are usually much more abundant in the sediments than harpacticoids. However, this numerical dominance of nematodes is rarely reflected in the diets of meiobenthivorous fish. Some of these fish species prey almost exclusively on harpacticoid copepods, excluding almost all other meiofaunal prey available (Coull 1990; Magnhagen et al. 2007). Comparative studies relating fish diets to meiofaunal prey in the sediments are rare (Alheit and Scheibel 1982; Sogard 1984; McCall 1992), resulting in a general lack of detailed information about prey selection or avoidance on meiofauna, especially with regard to the distribution and abundance of potential meiofaunal prey in the sediment at relevant temporal and spatial scales.

In this context, it has been argued (e.g. Gee 1989; Coull 1990) that feeding on harpacticoids appears to be highly selective. For instance, Alheit and Scheibel (1982) found selective feeding on *Longipedia helgolandica* Klie 1949 in a shallow lagoon of Bermuda. Sibert (1979) mentioned that *Harpacticus uniremis* Krøyer 1842 was consumed by salmon fry in British Columbia (Canada) in greater proportions than predicted from its abundance in the sediments, and Hicks (1984) found that juvenile flatfish feeding on intertidal sandflats in New Zealand fed exclusively on the harpacticoid *Parastenhelia megarostrum*.

Most habitats contain a variety of harpacticoid species, which may differ greatly in size, morphology, behaviour and microhabitat utilization (Hicks and Coull 1983). However, despite this diversity of potential harpacticoid prey species in the sediments, fish predators forage selectively. Selectivity in feeding behaviour has been experimentally investigated in small and juvenile fish (Feller et al. 1990; Aarnio 2000; Spieth et al. 2010), but the relative abundance of apparently preferred harpacticoid prey species in the field has not been taken into account for (Ellis and Coull 1989; Feller et al. 1990; Aarnio 2000). Consequently, essential knowledge whether feeding on harpacticoid prey is species-selective or merely on the most abundant harpacticoid species in the field is absent.

Therefore, the first aim of the present study was to investigate the general role of meiofauna in the sediment as a prey source for different small-sized demersal fish species. For this purpose, the seasonal variability of stomach

contents of solenette *Buglossidium luteum* (Risso 1810), the sand goby *Pomatoschistus minutus* (Pallas 1770), scaldfish *Arnoglossus laterna* (Walbaum, 1792), common dab *Limanda limanda* L. 1758 and plaice *Pleuronectes platessa* L. 1758 caught in a study area ("Box A") in the German Bight was analysed and related to size and species composition patterns of meiofauna obtained from benthos samples from the same location. Secondly, the occurrence of and the factors leading to prey selectivity were examined by comparing harpacticoid copepod species and size composition in both the fish diets and the sediment samples.

Materials and methods

Study area

The study area is located in the German Bight about 25 nautical miles north-west of the Isle of Helgoland and is part of the "German small-scale bottom trawl survey" (GSBTS; "Box A"; Ehrich et al. 2007) (Fig. 1). The mean depth of this area is 39 m, and water temperatures follow a seasonal cycle with monthly means between 4 and 17 °C. Temporary stratification occurs during summer, whereas the water column is otherwise well mixed. Sediments in the study area consist of >20 % mud (<63 μm fraction) in the south-west, gradually decreasing towards the north-east (0–5 % mud). The remainder of the sediments consists of sand (>63 μm fraction) (Ehrich et al. 2007).
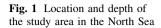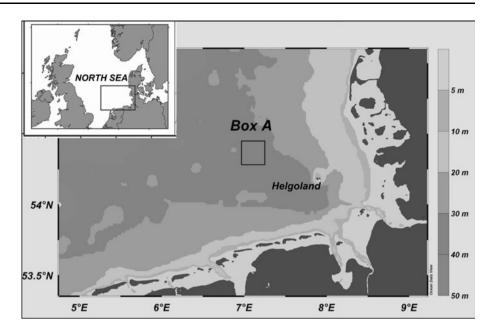
Sampling and sample treatment

Between January 2009 and January 2010, fish and meiofauna samples were obtained on research cruises with F.R.V. *Walther Herwig III* (January and July) and R.V. *Senckenberg* (May and October). With the exception of January 2009 (when only fish sampling was possible), fish samples were always taken at the same site and at the same time as the meiofauna samples. A total of 48 randomly assigned stations were sampled during daylight.

Meiofauna sampling

For meiofauna, two sediment samples were taken at each station using a 0.1 m² van Veen grab (only one in October because of stormy weather), as the multicorer did not close properly in the study area. The grab penetrated the sediment at a moderate speed; therefore, water flow through the corer was relatively unobstructed, and the bow wave was modest.

By penetrating the first 5-cm sediment (44.0 cm³) of one grab bucket with a cylindrical corer (diameter, 3.35 cm),

a subsample (8.80 cm^2) was taken to analyse the meiofauna community structure. In total, 69 sediment cores (18 cores in May, 22 cores in July, 9 cores in October and 20 cores in January 2010) were taken. Each core content was fixed on board in 10 % unbuffered formalin. In the laboratory, the fixed samples were washed through a sieve of 40-μm mesh size with filtered tap water.

Meiofauna and organic matter were extracted from sediment by gravity centrifugation with a colloidal silica polymer ($\rho = 1.17$ Levasil$^®$ 200/40 %) as flotation medium and kaolin to cover the heavier particles (McIntyre and Warwick 1984). The centrifugation was repeated three times at 4,000 rpm for 6 min, respectively. After each centrifugation, the supernatant was rinsed with tap water in a 40-μm sieve. The residual organic matter was transferred in a Bengal rose–stained 10 % formalin solution. Stained organisms were identified to lowest possible taxonomic level and counted separately. Harpacticoids similar in morphology were separated and fixed in glycerol on a prepared glass slide. Identification to species level was conducted using a *Leitz Dialux 22* microscope.

To obtain meiofaunal biomass data, all specimens (except harpacticoids and nematodes) were weighed wet to 0.0001 g precision. Biomass of harpacticoid copepods and nematodes was determined from volume calculations. From each species, the length × maximum width squared (in mm) was calculated and multiplied with a conversion factor to give body volumes in nanolitre. For the nematodes, a common factor of 530 was applied (Warwick and Price 1979). For the copepods, each species was categorized visually into one of eight body forms, and conversion factors were applied which were derived from scale models in plasticene (see McIntyre and Warwick 1984). The proportion of total biomass attributable to each species was calculated by multiplying the total numbers present by the adult body volume, assuming that the size distribution relative to the size of the adult is the same for each species, as is the conversion factor from volume to biomass.

Fish sampling

Fish sampling was performed with the Chalut á Grande Ouverture Verticale—GOV (except May and October)—and a standardized 2-m beam trawl. The GOV is the standard gear of the international bottom trawl survey in the North Sea (ICES 2009). The net opening was ca. 20 m wide and ca. 5 m high. Mesh size gradually decreased from 200 to 50 mm and a codend liner of 20-mm mesh opening (for details on the rigging see ICES 2009). The GOV trawl was towed 30 min with a constant speed of four knots over ground. Towing time started with bottom contact and vertical stabilization of the net opening.

The 2-m beam trawl carried a chain matt to prevent catching boulders and to enhance catch efficiency. It was fitted with a 20-mm stretched mesh and a codend liner of 4-mm knotless mesh. A detailed description of the beam trawl construction is given in Jennings et al. (1999). A SCANMAR depth sensor was attached to its top just behind the steel beam to determine the exact time and position of contact with the seabed. From the moment of contact with the seabed, the beam trawl was towed with a speed of 1.5–2 knots for 5 min.

From each haul, all individuals of *B. luteum*, *P. minutus*, *A. laterna*, *L. limanda* and *P. platessa* caught were counted, total length to the nearest cm (L_T) was measured, and wet weighed (M) was determined. For later stomach

analysis, if possible, a maximum of 35 individuals per species were frozen at −20 °C.

Stomach analysis

Because digestive enzymes in the stomachs still work after the death of a fish, a 30-min limit for preparation and weighing was applied after having the nets on board. Only the fish stomachs of the GOV hauls were immediately removed on board and frozen at −20 °C, whereas fish caught by the beam trawl were frozen whole without being dissected. In the laboratory, these fish were thawed, measured (L_T) and weighed (M) again before stomachs were removed.

In the laboratory, the contents of each stomach were rinsed in fresh water, and the prey items contained were divided into macro- and meiofaunal prey. For the macrofauna, each prey item was identified to lowest taxonomic level possible and counted. Reliable biomass data for each macrofaunal prey species were obtained from infauna samples taken simultaneously in the field during the same surveys. For the meiofauna, each prey item was identified to lowest taxonomic level possible and counted. All harpacticoid copepods found in the stomachs were fixed in glycerol on a prepared glass slide and identified to the lowest taxonomic level possible and counted.

Meiofaunal prey in fish stomachs are often strongly degraded, and reliable biomass data can be difficult to obtain. Therefore, the mean individual weights obtained for each species from the simultaneously taken sediment samples in the field were used to convert prey abundance into prey biomass of the stomach content after visual categorization into prey size classes.

Data analysis

The stomach contents of 672 *A. laterna* (L_T 2–14 cm), 1,557 *B. luteum* (L_T 2–15 cm), 752 *P. minutus* (L_T 2–7 cm), 1,402 *L. limanda* (L_T 3–31 cm) and 698 *P. platessa* (L_T 10–65 cm) were analysed. No detailed

analysis about fish predation on macrofaunal prey was made in the present study (predation on this group has been investigated by Schückel et al. 2011). Only the relative proportion of macrofaunal relative to meiofaunal prey was determined for each fish species. Individuals of *L. limanda* and *P. platessa* larger than 20 cm L_T were not included in further analysis since their diets were dominated by macrofaunal prey (for details see Schückel et al. 2011). Empty stomachs were not included in the diet analysis (Table 1).

The relative importance of each meiofaunal prey item in the sediment cores and in the stomach contents was expressed by (1) frequency of occurrence (I_O), (2) percentage of numerical abundance (I_N) and (3) percentage of biomass (I_W) for each season (Hyslop 1980).

To study the role of harpacticoids as prey source, the index of relative importance (R_I), which combines the relative contribution of a food item by number (I_N) and biomass (I_W), as well as by the percentage of frequency of occurrence (I_O), was calculated for each harpacticoid species in the sediment and in the stomachs, respectively, according to the following formula:

$$R_I = 100 \times \left(AI / \sum AI \right),$$

where AI (AI $= I_O + I_N + I_W$) is the absolute importance index.

Seasonal differences of harpacticoid communities in the sediment, as well as in the fish diets, were assessed using multivariate statistics of the PRIMER software package (Plymouth Marine Laboratory, PRIMER v6). A Bray–Curtis coefficient similarity matrix was calculated for both data sets consisting of non-transformed numerical abundances of each harpacticoid species recorded in the sediment cores and in the stomachs of each fish species. A one-way ANOVA (ANOSIM routine, test R) was performed to test the null hypothesis (i.e. no statistical differences in the sediment samples/fish diets between the seasons). Using a similarity of percentage analysis (SIMPER), characteristic harpacticoid species in the sediment and in the stomachs were identified for each season.

Table 1 Total number of stomachs analysed per season of the studied fish species

Species	Species code	Total number of stomachs									
		January 2009		May 2009		July 2009		October 2009		January 2010	
B. luteum	BUG	350	(0)	300	(4)	303	(8)	297	(24)	307	(92)
P. minutus	POM	153	(17)	146	(26)	37	(11)	334	(40)	82	(17)
A. laterna	ARN	159	(1)	31	(3)	71	(0)	225	(56)	186	(120)
L. limanda	LIM	171	(60)	50	(0)	277	(51)	166	(44)	192	(123)
P. platessa	PLE	81	(44)	27	(0)	100	(21)	111	(43)	37	(3)
$\sum$		914		554		788		1,133		804	

Number of empty stomachs is given in parentheses. Individuals of *L. limanda* and *P. platessa* with fish lengths >20 cm LT are excluded

To assess the relationship between the abundance of harpacticoid prey species in the sediment and the harpacticoid prey in the stomachs, the Ivlev (1962) selection index (E) was calculated per season:

$$E = (r_i - p_i) \times (r_i + p_i)^{-1},$$

where r_i is the relative abundance of prey species i in the stomachs and p_i is the relative abundance of prey species i in the sediment. E ranges from -1 to $+1$. Negative values indicate avoidance or inaccessibility of prey, and positive values indicate selection for a prey species. Non-selective feeding is indicated by values around zero.

Diet differences in harpacticoid prey selection between the studied fish species were tested using a one-way ANOVA based on numerical abundance data.

For examining size-related diet variations in harpacticoid prey selection, the percentage of frequency of occurrence and abundance of harpacticoid prey was determined per L_T for each fish species.

Results

Utilization of meiofauna by demersal fish

General composition and seasonality of meiofauna

In each season, harpacticoids were always the most frequently occurring meiofaunal prey group (I_O values range from 47 % in January to 57 % in October), whereas nematodes were always the most abundant prey group (I_N values range from 94 % in July to 97 % in October) (Table 2). Other frequently occurring meiofaunal groups were juvenile polychaetes in May ($I_O = 10$ %), copepodites

in July ($I_O = 8$ %), juvenile bivalves in October and January ($I_O = 10$ and 9 %, respectively) and ostracods in January (6 %), yet their numerical importance was low. In terms of biomass, harpacticoids and juvenile polychaetes were most dominant in each season (Table 2). Especially in summer, the meiofauna community was almost exclusively comprised by harpacticoids, doubling in biomass percentage ($I_W = 92$ %) compared to winter ($I_W = 66$ %) and spring ($I_W = 46$ %). The second most dominant meiofaunal group during summer were copepodites, reaching their highest biomass, frequency of occurrence and abundance in July ($I_W = 3$ %; $I_O = 8$ %; $I_N = 1$ %, respectively).

General composition and seasonality of fish diets

In terms of numerical abundance, meiofauna dominated the diets of *B. luteum* and *P. minutus* in all seasons, but was found rather season-specific in the diets of *A. laterna* and *L. limanda* (Fig. 2). In contrast, there was a complete absence of meiofaunal prey in the stomachs of *P. platessa* of any of the investigated size classes. Concerning prey biomass in the fish diets, macrofaunal prey generally dominated. A dominance in biomass of meiofaunal prey was only found for *B. luteum* in both winters (January 2009 and 2010).

The most important meiofaunal prey group of *B. luteum*, *P. minutus*, *A. laterna* and *L. limanda* were harpacticoids (Table 3). Over the course of the season, meiofauna dominated the diet of *B. luteum* in terms of occurrence as well as abundance by more than 80 % between January and July decreasing only slightly to about 60 % in the following October. Among different meiofaunal groups, almost exclusively harpacticoids were found numerically, gravimetrically as well as in terms of occurrence in each

Table 2 Percentage of frequency of occurrence (I_O), numerical abundance (I_N) and biomass (I_W) of meiofauna groups found in the sediment cores (8.80 cm²) per season

	May 09			Jul 09			Oct 09			Jan 10		
	I_O (%)	I_N (%)	I_W (%)	I_O (%)	I_N (%)	I_W (%)	I_O (%)	I_N (%)	I_W (%)	I_O (%)	I_N (%)	I_W (%)
Harpacticoids	**55.5**	1.8	**46.5**	**55.2**	3.9	**92.2**	**57.1**	1.2	**57.9**	**46.5**	3.8	**66.5**
Nematodes	**10.0**	96.2	2.2	**7.6**	93.9	**2.7**	**9.9**	97.3	2.4	**9.4**	94.2	**4.3**
Polychaetes	**10.0**	0.5	**42.5**	6.8	0.3	<0.1	**8.7**	0.3	**37.7**	7.3	0.1	**24.2**
Bivalves	**8.7**	0.5	0.4	**7.2**	0.3	0.6	**9.9**	0.6	0.3	**9.3**	0.1	1.1
Gastropods	–	–	–	2.4	0.2	<0.1	–	–	–	1.1	<0.1	1.2
Ostracods	0.6	0.1	<0.1	–	–	–	1.1	<0.1	0.2	6.3	<0.1	0.3
Echinoderms	–	–		5.2	<0.1	0.1	–	–	–	3.1	<0.1	0.2
Kinorhynchs	2.5	0.6	0.1	6.5	<0.1	0.1	7.7	0.6	0.4	6.3	<0.1	0.4
Harpacticoids copepodites	–	–	–	**8.0**	1.1	**3.4**	2.2	<0.1	0.7	<0.1	0.2	1.5
Others	14.6	0.9	8.0	9.2	0.3	1.0	5.6	<0.1	0.2	10.9	0.4	2.3
$\sum$ of cores studied	18			22			9			20		

Important values are marked in bold

Fig. 2 Percentage of
a numerical abundance and
b biomass of meiofaunal and
macrofaunal prey in the diet of
A. laterna (ARN), *B. luteum*
(BUG), *P. minutus* (POM),
L. limanda (LIM) and
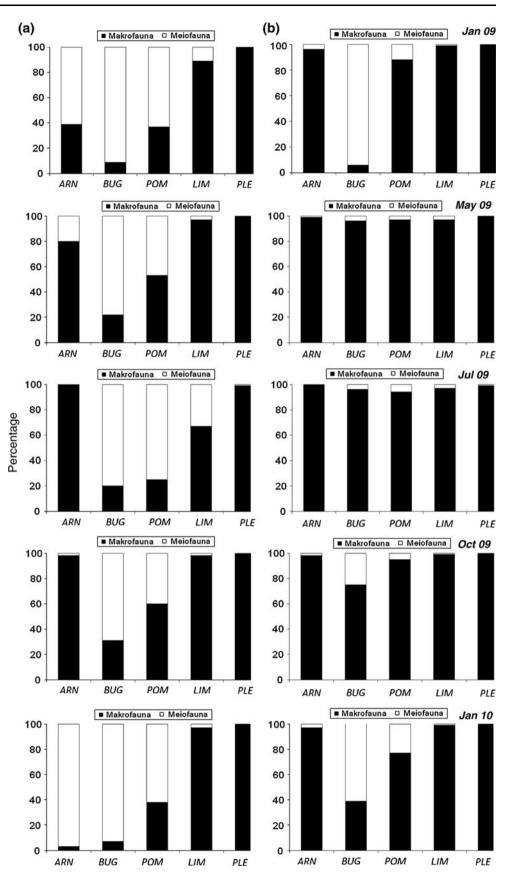*P. platessa* (PLE) per season

Table 3 Relative importance R_I (%) of harpacticoid copepod species found in the sediment cores (8.80 cm^2) per season and their seasonal contribution (%) to the harpacticoid assemblage indicated by SIMPER analysis (based on non-transformed abundance data)

Species	May 09		Jul 09		Oct 09		Jan 10	
	R_I (%)	Contrib (%)	R_I (%)	Contrib (%)	R_I (%)	Contrib (%)	R_I (%)	Contrib (%)
Ectinosomatidae								
H. canaliculatum	**20.7**	**30.7**	**14.2**	**10.7**	**26.9**	**26.8**	**15.5**	**12.8**
P. minor	**16.4**	**35.1**	**9.9**	**19.7**	**11.9**	**31.7**	**17.5**	**32.2**
Ectinosoma spp.	**12.2**	**6.3**	<0.1	<0.1	<0.1	<0.1	1.5	<0.1
Longipediidae								
L. coronata	**14.9**	2.1	**34.5**	**15.3**	**12.6**	1.1	1.9	<0.1
Ameiridae								
P. crassicornis	**8.1**	**14.5**	**5.1**	**10.7**	3.8	<0.1	**7.8**	**13.4**
Psyllocamptus spp.	<0.1	<0.1	0.8	<0.1	<0.1	<0.1	<0.1	<0.1
Idyanthidae								
T. reducta	**7.4**	**8.0**	**6.4**	**15.8**	**2.1**	**5.6**	**10.3**	**20.4**
T. minuta	<0.1	<0.1	<0.1	<0.1	2.1	<0.1	<0.1	<0.1
Miraciidae								
B. aemula	4.46	<0.1	4.2	<0.1	**12.9**	**26.5**	5.5	<0.1
D. reflexa	1.09	<0.1	–	–	–	–	–	–
Cletodidae								
C. limicola	1.6	<0.1	0.5	<0.1	–	–	**4.9**	**4.4**
C. tenuipes	–	–	0.4	<0.1	–	–	4.9	<0.1
Stylicletodes spp.	–	–	0.9	<0.1	–	–	–	–
E. propinquum	1.81	<0.1	**5.3**	**10.3**	4.4	2.1	**8.4**	**7.4**
E. gariene	–	–	–	–	1.4	<0.1	–	–
E. longifurcatum	–	–	–	–	3.1	1.1	**9.8**	**6.2**
Canuellidae								
Canuella spp.	3.28	<0.1	–	–	–	–	–	–
Tachidiidae								
Microarthridion spp.	0.75	<0.1	–	–	–	–	–	–
Rhizothricidae								
R. curvatum	–	–	–	–	4.0	<0.1	–	–
Siphonostomatoida	1.02	<0.1	–	–	–	–	–	–
Harpacticoids copepodites	–	–	**8.3**	**14.8**	2.5	<0.1	2.5	<0.1
Harpacticoids unident	6.2	2.1	9.3	3.7	12.4	5.9	9.5	3.2

Important values are marked in bold

season (Table 3). One exception was found in May with juvenile bivalves as the most frequently occurring prey group ($I_O = 74$ %), even though its biomass was low ($I_W = <1$ %).

For *P. minutus*, meiofaunal prey was most important in January (2009 and 2010) and July comprising the diet by more than 60 % in terms of occurrence as well as abundance (Fig. 2). Although the diversity of meiofaunal prey per season was generally higher in the diet of *P. minutus* compared to *B. luteum*, harpacticoids were both the most frequently occurring and the most abundant prey group, also exhibiting the highest biomass (Table 3). According to the three indices, the second

most important prey group in most months (May, July and January) were nematodes. Juvenile bivalves became an important prey group numerically, as well as in terms of occurrence, in May ($I_N = 21$ %; $I_O = 45$ %, respectively), similar to the diet of *B. luteum*. Ostracods were found regularly in the stomach contents in all seasons, but only in low numbers.

Clear seasonal differences in both the frequency of occurrence and abundance of meiofaunal prey were found in the diet of *A. laterna* and *L. limanda* (Fig. 2). Meiofauna dominated the diet of *A. laterna* in January and May, whereas the diet of *L. limanda* was mainly comprised of meiofauna in July. Among the meiofaunal prey groups,

harpacticoids dominated the diets of both fish species in each season according to the frequency of occurrence, abundance and biomass (Table 3). Juvenile bivalves became relevant in abundance for *A. laterna* in May (I_N = 28 %) and in terms of occurrence for *L. limanda* in May and July (I_O = 9 and 7 %, respectively). Ostracods were remarkably frequent in the diet of *L. limanda* in May (I_O = 20 %), being the second most important prey group in this month.

Pleuronectes platessa did not utilize meiofauna prey during the entire study period (Fig. 2). Therefore, *P. platessa* was excluded from subsequent analyses.

Selectivity in foraging

Harpacticoid copepods

In total, 19 different harpacticoid species belonging to 9 families were found in the study area. The most important family in the harpacticoid community was Ectinosomatidae, almost all belonging to the two species *H. canaliculatum* (Por 1964) and *P. minor* (Scott T. and A. 1894) (Table 4). Other important species that mainly contributed to the harpacticoid assemblage were *Pseudameira crassicornis* Sars, G.O. 1911 (Ameiridae), *Tachidiella reducta* Sars, G.O. 1909 (Idyanthidae) and *L. coronata* Claus, 1863 (Longipediidae).

Seasonally, the harpacticoid community structure differed significantly between May and July (ANOSIM, $R = 0.52$, $p = 0.0001$) and July and October (ANOSIM, $R = 0.60$, $p = 0.0001$) (Table 5). *P. minor* and *H. canaliculatum*, even though both are characteristic species in the harpacticoid community in all seasons, contributed differently in different seasons with more than 35 % from October to May, but decreasing in July to 28 %. A similar seasonal pattern for these two harpacticoid species was found using the importance index (R_I), which combines beside percentage of abundance also frequency of occurrence and biomass (Table 4). In contrast, an opposite trend with the highest abundances as well as importance values in summer and lowest in winter was found for *L. coronata* and copepodites. Particularly in summer, the harpacticoid community was mainly characterized by *L. coronata* as the most important species (R_I = 35 %).

Beatricella aemula (Scott T. 1893) was most important in the harpacticoid community in October, whereas *Cletodes limicola* Brady 1872 and *Enhydrosoma longifurcatum* Sars, G.O. 1909 were most important in the harpacticoid community in winter. No general seasonal trends according to the R_I index were found for *P. crassicornis*, *T. reducta* and *Enhydrosoma propinquum* (Brady and Robertson in Brady 1880).

Table 4 One-way analysis (ANOSIM) between harpacticoid copepod communities in the sediment cores (8.80 cm^2) per season based on non-transformed abundance data

Groups/test	R statistic	Significance level
Sediment cores		
Global test		
All seasons (Jan, May, Jul, Oct)	0.35	0.001
Pairwise test		
Jan, May	0.24	0.005
Jan, Jul	0.28	0.001
Jan, Oct	0.43	0.002
May, Jul	**0.57**	0.001
May, Oct	0.30	0.001
Jul, Oct	**0.58**	0.001

Bold values are significant

Prey selection of harpacticoid copepods

In total, eight different harpacticoid species belonging to six families were found in the stomach contents. The most important families in the diet of all the four fish species were Ectinosomatidae, belonging almost entirely to the species *Pseudobradya* spp. and *H. canaliculatum,* and Longipediidae, belonging exclusively to *Longipedia* spp. (Table 6). Families such as Ameiridae, Idyanthidae and Miraciidae were generally of low importance in the fish diets, although they occurred in the sediment cores.

Significant differences in the abundance of harpacticoid species were found in all studied fish diets (Table 7). For *B. luteum*, the harpacticoid community in the winter diet 2009 differed significantly from that in all other seasons (Table 7). This was attributed to *Pseudobradya* spp., the most abundant prey species in January 2009 (R_I = 98 %), and *Longipedia* spp., the most abundant prey species between May and October (R_I > 90 %, respectively). A high positive selection was found for *Pseudobradya* spp. in January 2010 and *Longipedia* spp. between May and October (Table 6). High E values of *H. canaliculatum* as well as *T. reducta* in January only indicated a strong selection for these two species during winter.

A similar seasonal trend of diet differences in harpacticoids was found in the stomachs of *P. minutus*, even though less distinct compared to *B. luteum* (Tables 6, 7). *Pseudobradya* spp. was the most important harpacticoid in the diet of both winters (R_I = 47 % and 54 %) and was replaced by *Longipedia* spp. between spring (R_I = 97 %) and autumn (R_I = 57 %). Highly positive values of Ivlev's index for *Pseudobradya* spp. in autumn and winter and for *Longipedia* spp. during summer indicated prey selection, whereas the negative E values of *Pseudobradya* spp. in spring and summer indicated avoidance. Apart from *E. propinquum* in winter, cletodid species were always selected against.

Table 5 Percentage of frequency occurrence (I_O), numerical abundance (I_N) and biomass (I_W) of meiofauna prey groups found in the diet of the studied fish species per season

Prey groups	Jan 09			May 09			Jul 09			Oct 09			Jan 10		
	I_O (%)	I_N (%)	I_W (%)	I_O (%)	I_N (%)	I_W (%)	I_O (%)	I_N (%)	I_W (%)	I_O (%)	I_N (%)	I_O (%)	I_N (%)	I_W (%)	I_W (%)
B. luteum															
Harpacticoids	**66.6**	**96.5**	**99.9**	**26.4**	**76.1**	**99.9**	**89.8**	**99.7**	**99.9**	**98.9**	**99.8**	**99.9**	**92.6**	**99.3**	**99.9**
Bivalves	**33.4**	3.5	0.1	**73.6**	**23.9**	0.1	10.2	0.3	0.1	1.1	0.2	0.1	7.4	0.3	0.1
Number of stomachs	350			296			295			273			215		
P. minutus															
Harpacticoids	**78.9**	**72.2**	**97.0**	**60.8**	**20.1**	**98.2**	**81.7**	**58.9**	**99.0**	**92.0**	**98.1**	**97.1**	**72.9**	**78.2**	**97.1**
Bivalves	–	–	–	**45.4**	**21.2**	0.2	–	–	–	3.2	1.5	0.3	–	–	–
Ostracods	1.3	0.6	0.5	**9.1**	**8.2**	0.4	3.9	0.6	0.3	3.2	0.4	3.4	2.1	0.4	0.2
Nematodes	21	**27.4**	2.8	27.3	72.8	1.8	**11.5**	**40.5**	1.1	–	–	–	**16.7**	**21.2**	2.8
Number of stomachs	136			120			26			294			65		
A. laterna															
Harpacticoids	**93.7**	**88.3**	**99.8**	**92.9**	**72.0**	**99.9**	–	–	–	**100**	**100**	**100**	**100**	**100**	**100**
Bivalves	6.3	11.7	0.2	7.1	**28.0**	0.1	–	–	–	–	–	–	–	–	–
Number of stomachs	158			28			71			169			66		
L. limanda															
Harpacticoids	**94.2**	**96.4**	**99.8**	**79.5**	**90.9**	**99.7**	**90.3**	**98.5**	**99.8**	**97.7**	**99.4**	**99.9**	**92.6**	**95.5**	**99.9**
Bivalves	5.8	3.6	0.2	**9.3**	1.1	0.2	**7.2**	1.5	0.2	2.3	0.6	0.1	7.4	4.5	0.1
Ostracods	–	–	–	**20.0**	9.1	0.1	–	–	–	–	–	–	–	–	–
Number of stomachs	111			50			226			122			69		

Important values are marked in bold

Only two harpacticoid species, namely *Pseudobradya* spp. and *Longipedia* spp., comprised the diet of *A. laterna* as well as of *L. limanda* during the study period (Table 6). There were significant seasonal differences in the diets in both fish species (Table 7). According to R_I values, *Pseudobradya* spp. was of greatest importance in the diet of *A. laterna* in January and May 2009, whereas *Longipedia* spp. was most important from October to January 2010 (Table 6). In the diet of *L. limanda,* both harpacticoids were found with highest R_I values for *Pseudobradya* spp. in January (2009 and 2010) and for *Longipedia* spp. in May and July. This contrasting prey selection between *A. laterna* and *L. limanda* on both harpacticoids was also shown by Ivlev's selection index, being positive for *Pseudobradya* spp. in spring (*A. laterna*) and winter (*L. limanda*), whereas positive values for *Longipedia* spp. were found in summer (*L. limanda*) and autumn (*A. laterna*, *L. limanda*).

Size aspects

A decreasing frequency of occurrence of harpacticoid prey with increasing fish length L_T was found in the diet of all studied fish species (Fig. 3). A similar trend in harpacticoid abundances was found for *B. luteum, A. laterna* and *L. limanda*, whereas the numerical utilization of harpacticoids by *P. minutus* was largely independent of fish size (4–7 cm L_T) ($I_N = 20$ %). Highest abundances of harpacticoids were found in the diet of *B. luteum* below 9 cm L_T, in the diet of *P. minutus* and *A. laterna* between 3 cm and 4 cm L_T and in the diet of *L. limanda* of $L_T = 7$ cm.

On the basis of these results, it should be noted that no individuals of *P. platessa* below 10 cm L_T were caught in the present study. However, meiofauna was previously found to be an important prey in small-sized plaice between fish lengths of 4 and 10 cm L_T (Gee 1989).

Discussion

Numerically, meiofaunal prey dominated the diet of *B. luteum* and *P. minutus* in all seasons, was found seasonally in the diet of *A. laterna* and *L. limanda* and was absent in the diet of *P. platessa* between 10 and 20 cm body size. Thus, although sharing the same habitat, seasonal differences in meiofauna prey resources do exist between these small-sized demersal fish species. In terms of prey biomass, macrofaunal prey dominated in all fish diets reflecting the

Table 6 Relative Importance R_I (%), Ivlev's selectivity index (E) and level of selection of harpacticoid species found in the diet of the studied fish species

	Jan 09	May 09			Jul 09			Oct 09			Jan 10		
	R_I (%)	R_I (%)	E	Level of selection	R_I (%)	E	Level of selection	R_I (%)	E	Level of selection	R_I (%)	E	Level of selection
B. luteum													
Longipedia spp.[b]	1.9	94.2	0.7	++	98.0	0.5	++	94.5	0.8	++	47.1	0.7	++
H. canaliculatum	<0.1	3.3	0.9	++	–	–	– –	2.3	–0.7	– –	9.5	1	++
Pseudobradya spp.[a]	98.1	2.3	–0.7	– –	<0.1	–0.9	– –	2	0.7	– –	34.7	0.3	++
P. crassicornis	<0.1	<0.1	–1	– –	<0.1	–1	– –	<0.1	–1	– –	1.0	–0.8	– –
B. aemula	–	<0.1	–1	– –	1.0	1	++	0.2	–0.9	– –	–	–	
T. reducta	–	–	–		–	–		0.2	–0.9	– –	5.9	1	++
P. minutus													
Longipedia spp.	47.6	96.6	0.7	++	78.8	0.4	++	57.1	0.6	++	33.0	0.5	++
H. canaliculatum	–	–	–		11.4	1	++	<0.1	–1	–	–	–	
Pseudobradya spp.[a]	47.0	3.4	0.6	– –	9.6	0.1	0	42.1	0.6	++	53.9	0.5	++
E. propinquum	2.7	<0.1	–1	– –	<0.1	–1	– –	<0.1	–1	– –	7.5	1	++
C. tenuipes	2.1	–	–		<0.1	–1	– –	–	–		5.5	0.1	0
A. laterna													
Pseudobradya spp.[a]	99.9	99.8	0.8	++	<0.1	–0.9	– –	<0.1	–1	– –	<0.1	–1	– –
Longipedia spp.[b]	<0.1	<0.1	–1	– –	<0.1	–0.9	– –	99.8	0.8	++	99.7	0.9	++
L. limanda													
Pseudobradya spp.[a]	99.8	12.8	–0.1	0	<0.1	–1	– –	15.9	0.1	0	99.8	0.7	++
Longipedia spp.[b]	<0.1	87.1	0.7	++	99.1	0.5	++	84.1	0.7	++	<0.1	–1	– –

++ positive selection, – – negative selection, 0 no selection. For Jan09 only R_I values are given because only fish stomachs were sampled, not meiofauna in the field

[a] Mainly P. minor

[b] Furca missing. Completed individuals were mostly identified as L. coronata and L. scotti

Table 7 One-way analysis (ANOSIM) of harpacticoid copepod composition in the fish diets (based on non-transformed abundance data)

Groups/test	R statistic				Significance level			
Stomach contents	BUG		POM		ARN		LIM	
Global test								
All seasons (Jan 09, May, Jul, Oct, Jan 10)	**0.83**	0.001	0.31	0.001	0.34	0.016	**0.58**	0.007
Pairwise test								
Jan 09, May	**1**	0.001	0.45	0.002	0.38	0.210	**1**	0.330
Jan 09, Jul	**1**	0.001	**0.54**	0.008	**1**	0.001	**1**	0.018
Jan 09, Oct	**0.99**	0.001	0.07	0.175	0.40	0.430	**1**	0.330
Jan 09, Jan 10	0.39	0.001	0.12	0.075	0.38	0.210	0.45	0.330
May, Jul	**0.81**	0.001	0.19	0.088	**1**	0.001	0.13	0.320
May, Oct	0.42	0.004	0.27	0.003	0.21	0.330	0.1	0.500
May, Jan 10	0.48	0.005	**0.61**	0.001	**0.50**	0.005	0.13	0.330
Jul, Oct	0.39	0.004	0.21	0.071	**1**	0.001	0.48	0.050
Jul, Jan 10	**1**	0.001	**0.71**	0.005	**1**	0.001	**0.60**	0.050
Oct, Jan 10	**0.94**	0.001	0.30	0.007	0.01	0.005	0.25	0.500

Species codes of the studied fish species are explained in Table 1

Bold values are significant

Fig. 3 Percentage of **a** frequency of occurrence and **b** abundance of harpacticoid prey per fish length L_T of the studied fish species

higher weight of macrofaunal compared to meiofaunal prey. For details on fish predation on macrofaunal prey groups, see Schückel et al. (2011) and Schückel et al. (2012).

Among different meiofaunal prey groups, harpacticoids were always of primary importance in the diet of each of the studied fish species during all seasons, whereas nematodes dominated the meiofauna community in the study area.

The meiofauna community in the study area

Nematodes were always the dominant meiofauna group in sediment samples in terms of abundance, while harpacticoids occurred most frequently. Seasonal differences were negligible for meiofaunal abundance but significant for biomass, due to a marked increase in harpacticoids in summer.

Previous research on meiofauna communities in the North Sea has also shown that nematodes are the dominant meiofauna group in terms of abundance accounting for at least 90 % of the total meiofauna (Juario 1975; Heip and Craeymeersch 1995). Their densities ranged from 61 to 4,167 ind./10 cm² and they were especially abundant in the southern North Sea (Huys et al. 1992). Harpacticoids ranked second in abundance, whereas other groups such as polychaetes, kinorhynchs, gastrotrichs, bivalves and ostracods were far less abundant (Juario 1975; Govaere et al. 1980; Heip et al. 1992; Heip and Craeymeersch 1995). Seasonally, meiofauna abundance generally peaks in spring and summer following an increase in food supply after the spring phytoplankton bloom, whereas abundance is low during autumn and winter, when most meiofauna groups

live deeper in the sediment (Olafsson and Elmgren 1997). Only harpacticoids are known to occur most of the year, concentrated in the upper six centimetre of the sediment (Huys et al. 1986). However, in the area of investigation in the German Bight ("Box A"), seasonal changes of both abundance and occurrence of meiofauna groups were small. Only an increase in copepodite occurrence as well as of harpacticoid biomass was found during summer, probably triggered by reproductive activities of harpacticoid copepods and sufficient food supply due to phytoplankton sedimentation after the spring bloom (Rudnick et al. 1985).

Confirming previous results of the North Sea Benthos Survey (for details see Huys et al. 1992), epibenthic species belonging to the family Ectinosomatidae (mainly *H. canaliculatum* and *P. minor*) and Longipediidae (mainly *L. coronata*) dominated the harpacticoid community structure in the study area. The pelophilic species *P. crassicornis* (Ameiridae) as well as *T. reducta* (Idyanthidae) were also important in this community. In contrast, interstitial species were completely absent in the present study, although interstitial species belonging to the family Leptastacidae (mainly *Leptastacus* and *Paraleptastacus*) were described as characteristic species in previous studies (Heip et al. 1992). *Leptastacus* and *Paraleptastacus* are both known as interstitial sliders (Huys et al. 1992), probably able to penetrate deeper into the sediment than the first five centimetre, which were sampled here.

Seasonally, abundances of Ectinosomatidae and Longipediidae differed significantly, being highest for *P. minor* and *H. canaliculatum* between October and May but lowest in July, whereas the reverse with a peak in abundance in July was found for *L. coronata*.

Such seasonal changes of harpacticoid densities are mostly observed in vertical distribution patterns, which are caused by migrations in response to seasonal fluctuations in environmental parameters (e.g. oxygen, salinity) and physiological adaption such as changes in growth rate and fecundity in response to environmental pressures. More details in terms of species-specific migration patterns in harpacticoids will be given in the section below directly related to its function as potential prey source for the studied demersal fish.

Meiofauna as prey source of demersal fish

Diets of *B. luteum* and *P. minutus* were numerically dominated by harpacticoids during all seasons. Such a dominance of harpacticoid prey throughout the seasons has also been reported for *B. luteum* in the Western Mediterranean (Tito de Morais and Bodiou 1984) and the Scottish coast (Nottage and Perkins 1983) and for several gobiid species in the North Sea (Zander 1979), in the Adriatic Sea (Kovačić 2001, 2007; Kovačić and la Mesa 2008) and in

the Gulf of Mexico (Fitzhugh and Fleeger 1985). Other meiofaunal prey groups (juvenile bivalves, ostracods and nematodes) became important in their diets only in May, indicating a seasonal change in prey preferences during spring. Constrained by their small mouth gapes and a more sediment surface-orientated feeding strategy, *B. luteum* and gobiids catch very small benthic prey buried in the top few centimetres of the sediment or living very close to the sediment surface, which represents the habitat of most harpacticoids (Tito de Morais and Bodiou 1984; Darnaude et al. 2001). Furthermore, their caloric values are 35 % higher than those of most other meiofaunal groups (Gee 1989). Consequently, the relatively low costs of capturing harpacticoids and their relatively high caloric content turn them into a more energy-efficient prey. However, the seasonal trend to meet energy requirements in spring also by eating other meiofauna prey groups (e.g. bivalves) as well as macrofauna was also confirmed for *P. minutus* in the Baltic Sea, even though harpacticoids always comprised the most important prey group in each season (Aarnio and Bonsdorff 1993).

Meiofauna was more important as a seasonal prey source in the diet of *A. laterna* and small-sized *L. limanda*. Meiofauna mainly characterized the diet of *A. laterna* during winter, dominated by harpacticoids in terms of occurrence as well as abundance. In contrast, harpacticoids dominated the diet of *L. limanda* spring and summer. Similar to both fish species discussed before, juvenile bivalves became an important prey group in spring. On the basis of their mouth morphology, it can be assumed that *A. laterna* and *L. limanda* are able to feed on larger and hence more energetically valuable prey (Piet et al. 1998; Schückel et al. 2011, 2012). Consequently, mainly macrofaunal prey (e.g. crustaceans and polychaetes) comprised the diets of both fish species, whereas meiofaunal prey seems to be of less diet importance. Confirming this, preferential feeding on macrofauna was also found in previous diet studies for both fish species (e.g. Gibson and Ezzi 1980; Bayan et al. 2008; Schückel et al. 2011) and furthermore, was already found in relatively small fish (L_T's < 10 cm; Schückel et al. 2012).

However, a reduced feeding activity of *A. laterna* in winter resulting in low stomach functions and low mobility, together with a reduced availability of larger benthic prey in the field, may have caused the observed increasing numbers of harpacticoids in the January stomachs. Assuming for dab a rather weak condition in spring after the winter feeding pause and the spawning period (Knust 1986; Hinz et al. 2005), harpacticoids may also provide an easily available and nutritious prey to fulfil energy requirements.

Increasing abundances of juvenile bivalves in all fish diets in May indicated a match with spawning periods of bivalves in this area (Beukema et al. 1998; Reiss and

Kröncke 2004). The subsequent decrease of juvenile bivalves in occurrence, abundance and biomass in the field during summer might be due to predation pressure of the studied fish species. Similar results of a strong predation pressure on juvenile bivalves after spawning was also found for small plaice in the Baltic Sea (Olafsson and Elmgren 1997) and for gobiids in the Adriatic Sea (Kovačić and la Mesa 2008). Thus, seasonal changes of meiofauna in the diet composition of small demersal fish could be the result of seasonal availability of suitable meiofaunal prey (see Tables 2, 3).

Although nematodes represented, depending on season, between 93 and 98 % of the total number of individuals in the sediment, they were completely absent in the flatfish diets but, interestingly, they occurred in almost each season in the diet of *P. minutus* (see Table 5). This agrees well with the literature showing that harpacticoids are usually the most abundant prey group in the fish diets, whereas nematodes dominate the sediment (e.g. Gee 1989 and references therein). Food selection of demersal fish depends on the availability of the prey, which is mainly determined by its density, visibility, accessibility and mobility (Nelson and Coull 1989). Feeding of the studied fish on meiofauna was mainly focused on harpacticoids living on or near the sediment surface, whereas nematodes have a deeper vertical distribution (Aarnio and Bonsdorff 1993; Aarnio 2000). Another factor that may explain the absence of nematodes in the stomachs could be differences in digestion rates for these two taxa. Harpacticoids have an exoskeleton that is slowly digested and remains in the gut for several hours after ingestion, while nematodes are soft-bodied and are digested rapidly (Alheit and Scheibel 1982; Scholz et al. 1991), thus probably giving a false impression of diet composition. A third explanation implies that physical disturbance caused by searching fish in the sediment may have suspended nematodes from the uppermost sediment layer or swept them away (Fitzhugh and Fleeger 1985; Gee 1989). This last explanation, regarding our study, also indicates best why, on the one hand, nematodes are absent in the flatfish diets, but on the other hand, are a dominant prey item in the goby diet. Similar findings of nematodes in gobiid stomachs were also reported for *P. minutus* and *P. lozanoi* in the North Sea (Fonds 1973) as well as for two closely related gobiids in the Gulf of Mexico (Fitzhugh and Fleeger 1985). The latter assumed that gobies graze sediments more or less indiscriminately in addition to sight feeding for larger prey. This rather passive feeding strategy in searching prey may contradict with a more active visual feeding strategy of flatfish remaining motionless on the bottom at first, and then periodically lunging rapidly forward, causing the upper sediment layers to float in suspension (de Groot 1971; Hoghue and Carey 1982). Also morphological differences

(e.g. body shape, mouth gape) between gobiids and pleuronectids may enable *P. minutus* to penetrate in deeper sediments.

Prey selectivity

Fish predation on harpacticoids was highly selective for the two species *Pseudobradya* spp. and *Longipedia* spp. *Pseudobradya* spp. was found almost exclusively in fish stomachs in winter, whereas *Longipedia* spp. dominated the stomach contents between spring and autumn.

Selective feeding on harpacticoid species seems to be common in many fish species. For instance, Alheit and Scheibel (1982) showed exclusive feeding on *L. helgolandica* by predatory fishes in a Bermudan lagoon. Hicks (1984), in his study of flatfish feeding on intertidal sandflats in New Zealand, also found exclusive feeding on one harpacticoid species (*P. megarostrum*). For *B. luteum* from the Mediterranean, a marked preference for *Pseudobradya beduina* was described, whereas the goby *D. quadrimaculatus* from the same habitat fed exclusively on *H. canaliculatum* (Tito de Morais and Bodiou 1984).

Firstly, by comparing the meiofauna community in the sediment with that in the fish stomachs, it becomes clear that the studied fish species fed almost exclusively on the most abundant harpacticoids in the sediment. Thus, fish predation on *Pseudobradya* spp. in winter and *Longipedia* spp. in summer may merely reflect their high prey densities in the field. Contradictory to this, Ivlev's high selection values for all studied fish species on both harpacticoids clearly suggested a positive prey selection.

Secondly, harpacticoids differ in vertical distribution within the sediment. By dwelling in the uppermost sediment layers, *Pseudobradya* spp. and *Longipedia* spp. are more vulnerable to predation compared to deeper interstitial or burrowing species (Gee 1987). Consequently, interstitial species, such as *B. aemula* (also known to build a tube into which it retreats when disturbed; Huys et al. 1986) and *E. propinquum,* were negatively selected. Only the upward migration in the sediment of *B. aemula* during summer leads to an increase in fish predation (Huys et al. 1986), explaining the positive prey selection for this harpacticoid in the diet of *B. luteum* only in July.

Moreover, *Pseudobradya* spp. and *Longipedia* spp. are both emergers, swimming into the overlying water (typically during the night) and returning to the seabed during the day (Sedlacek and Thistle 2006). Thus, *Pseudobradya* is classified as a moving water emerger during all seasons, whereas *Longipedia* moves in the water column mainly in summer (Thistle 2003), leading to a greater susceptibility of *Longipedia* sp. for visual predators during summer. Diets of the studied fish species changed towards an intensively feeding on *Longipedia* spp. in July, even though *Pseudobrayda* spp. also occurred in high abundances in the

sediment. In this context, prey selection on *Longipedia* spp. could also be prey size dependent. *Longipedia* spp. is significantly larger (mean length, 0.9 mm; own data), compared to *Pseudobradya* spp. (mean length, 0.4 mm; own unpubl. data), and consequently more favourable as a source of energy compared to *Pseudobrayda* spp. Such a prey size selection was also found by McCall (1992) for juvenile flounder, mainly feeding on the largest available harpacticoids.

Size aspects

The relative contribution of meiofauna and macrofauna to the diet composition of fish depends mostly on predator size (e.g. Gee 1989; Kovačić and la Mesa 2008; Schückel et al. 2012). On the basis of the optimal foraging theory, smaller fish eat smaller prey and switch usually to larger prey to maximize their net energy gain as fish length increases (Schoener 1971). Confirming this, harpacticoids as the prevalent meiofaunal prey rapidly decreased in terms of frequency of occurrence as well as numerical abundance in the diets of all studied fish species with increasing fish size. Interestingly, threshold lengths at which the importance of harpacticoid prey decreased differed for the studied species. The abundance of harpacticoid prey decreased already at relatively small individual size in *A. laterna* and *P. minutus* (3–4 cm L_T), whereas they were still abundant prey for *B. luteum* also at larger fish sizes (8 cm L_T). Similar results were described for gobies *B. affinis* in the Adriatic Sea (Kovačić and la Mesa 2008) and for *P. minutus* in the Baltic Sea (Aarnio and Bonsdorff 1993), indicating significant differences between the diet of large- and small-sized individuals, switching from meiofaunal to macrofaunal prey at approximately 3–4 cm L_T, respectively. Harpacticoids in the diet of the goby *D. quadrimaculatus*, still constituting 50 % in the total diet at 3 cm fish length, decrease to almost 0 % in individuals up to a fish length of 5 cm (Tito de Morais and Bodiou 1984). Predominant feeding on harpacticoids was also found in *A. laterna* as well as for the closely related *A. thorni* with L_T's between 5 and 6 cm, but changing rapidly towards polychaetes and fish prey at larger size (Bayan et al. 2008). In contrast, for a *B. luteum* population on the Scottish coast, harpacticoids were still an important prey in the diets of individuals reaching fish lengths of 8 cm L_T (Nottage and Perkins 1983). Mainly morphological constraints (e.g. mouth gape, jaw structures) determine the threshold length for fish below which meiofauna are of no value as prey. In most flatfish species and gobiids, this threshold length is about 3 cm (total fish length). Above this size, macrofauna are always the dominant prey, whereas below this size, harpacticoids can constitute between 20 and 100 % (Gee 1989). Mouth gape widths differed between the studied fish species, being generally larger for *P. minutus* and

A. laterna and smaller for *B. luteum* (Piet et al. 1998). Consequently, harpacticoids as prey resource were also used by *B. luteum* at larger fish sizes.

Conclusion

Our results indicate that predation on meiofauna by solenette, goby, scaldfish and dab is highly selective for harpacticoids during all seasons, with a clear focus on species living in the uppermost sediment layers. It remains unclear whether the predation pressure induced by the fish species investigated here affects the meiofauna community in the study area. Several studies, both under laboratory and field conditions, found no or only small effects on meiofauna abundances by fish predation, since rapid turnover rates and short generation times of the meiofauna may compensate for the predation effects. Other factors, such as predatory meiofauna and macrofauna as well as physical properties, are more important in structuring meiofauna assemblages (Alheit and Scheibel 1982; Gee 1987; Coull 1990; Service et al. 1992; Aarnio 2000). Other authors have, however, demonstrated significant reductions in meiofaunal abundance in response to predation by fish (several flatfish species, gobiids and juvenile spot) (e.g. Bell and Coull 1978; Tito de Morais and Bodiou 1984; Fitzhugh and Fleeger 1985; Ellis and Coull 1989). They suggested that although fish predation alone does not control the distribution and overall abundance of meiofauna species, predator–prey interactions are important factors in controlling particular meiofaunal prey species. Therefore, we hypothesize that an intensive selective feeding of the four fish species on *Pseudobradya* spp. and *Longipedia* spp., combined with predation of other epibenthic predators (e.g. shrimps), might have an impact on the harpacticoid community, whereas predation impact on the meiofauna as a whole might be even negligible.

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