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Trophic interactions between preadult and adult *Pomatoschistus minutus* and *Pomatoschistus microps* and young *Platichthys flesus* occurring in inshore waters of the Gulf of Gdańsk (Southern Baltic)

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Key words: feeding, flounder, goby, Baltic Sea, inshore waters

Abstract

We intended to estimate if shallow inshore waters of the Gulf of Gdańsk can be considered important feeding grounds for the fishes under investigation. We also examined whether competition for food exists between the investigated fishes which co-exist. The study was carried out at Sopot and Chałupy stations from summer 2001 to autumn 2003. The results showed the high importance of *Neomysis integer,* which exclusively lives in coastal waters, in the diet of all three investigated fish species. It indicates that they utilize this zone as a feeding ground. The obtained dataset also led to the conclusion that fish trophic niches overlap by about 40%.

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INTRODUCTION

In food web studies analysis of stomach content are essential to understanding the role of fish in an ecosystem. The non-tidal Baltic Sea, with low salinity, marked seasonality and a relatively simple ecosystem dominated by only a few species, provides a specific environment for fish living there and many trophic interactions between the fish have not been fully investigated. The shallow, soft bottoms are important feeding habitats (Aarnio 2000), but due to some abiotic (e.g. salinity, temperature) changes in the coastal areas, prey availability can be unpredictable. This situation offers an opportunity for assessing competitive interactions under stressful, exceptional conditions.

On shallow, sandy bottoms the number of trophic niches is low and because of this the fish species which simultaneously inhabit such areas are likely to exploit a common pool of resources and occupy relatively broad niches with wide overlaps (Evans, Tallmark 1985). Describing coexisting species, the habitat, food and time, in decreasing order, should be considered as the most important separating niche dimensions (Schoener 1974).

Most studies associated with shallow inshore Baltic waters have concentrated on the diet of a single species, e.g. Hesthagen 1977 and Jackson et al. 2002, or have investigated only commercial fishes, e.g. Mańkowski 1947, Mulicki 1947, Malorny 1990, Ostrowski 1997. Trophic interactions in this specific zone are not well documented in the Polish literature and have been scarcely studied.

This study intended to answer the question of the significance of inshore waters of the Gulf of Gdańsk as a feeding ground and to investigate the importance of various prey in the food composition of investigated fishes. This paper also examined whether competition for food exists between co-existing fish in the shallow water zone.

MATERIALS AND METHODS

The study was carried out in the Gulf of Gdańsk, from summer 2001 to autumn 2003 at Sopot station and in autumn 2003 at Chałupy station (Fig. 1). The fish were taken at the depth of 1 meter, on the 100 m distance along the coastline. The catches, at every investigated place, were made using a hand trawl with a horizontal opening of approximately two meters and a mesh size of 6 millimeters (in cod end 1 millimeter). Sampling places and hours were the same for all trawlings at each station. After fish collection, for stomach and gut analysis, we preserved them in a 4% buffered formaldehyde solution. The time between catching and preserving the fish was short, so that further digestion of the stomach contents could be avoided. The total length (*longitudo totalis*) of

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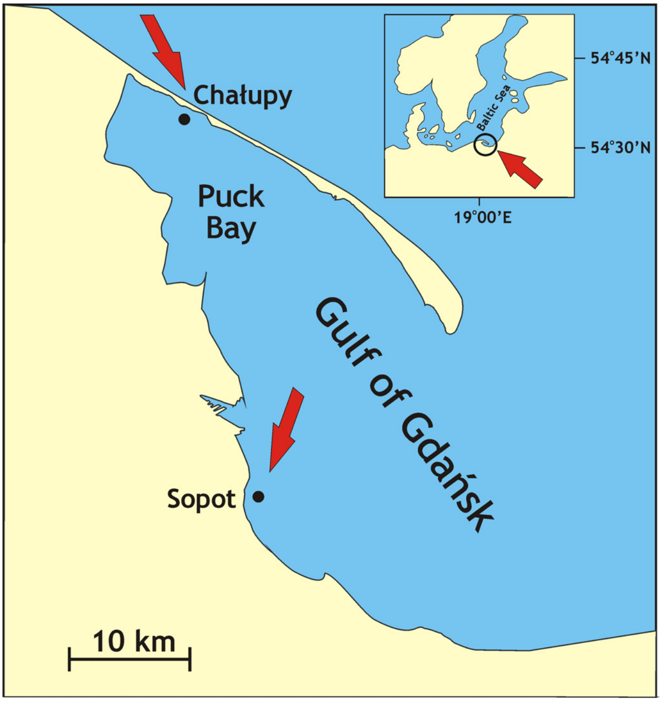

Fig. 1. Study area and sampling places.

individuals from all three investigated fish species was determined to 1 mm and the weight to 0.01 g. The entire contents of fish intestines were removed and determined to the lowest possible taxon. Identifiable prey specimens were counted and measured under a stereomicroscope and their wet weight was calculated using length-weight relationship (Witek 1995, Berestovsky et al. 1989). The diet data were analyzed in terms of frequency of occurrence, quantity and weight of prey in fish stomachs. Then, they were presented as "index of relative importance" (IRI, Pinkas et al. 1971) and expressed on a percent basis.

$$IRI = (\%N + \%Vol) \times \%F \quad (1)$$

where:

%N - percentage of food item quantity in the fish with non-empty stomachs;
%Vol - percentage by volume of food item in the fish with non-empty stomachs;
%F - frequency of occurrence of the food item in the fish with non-empty stomachs.

Aiming at detecting differences between niche conditions we compared the IRI index for the flounder which appeared in catches from autumn 2003 at both investigated stations.

The degree of similarity in food choice between the sand goby, the common goby and the flounder from Sopot and Chałupy stations, which contained different sets of dominant food items, was investigated in seasons when at least two of the above mentioned species occurred in catches (summer 2001, autumn 2001, spring 2002, summer 2002, spring 2003, autumn 2003 - Chałupy station). Food-niche overlap was estimated according to the equation given by Hurlbert (1978):

$$C_{xy} = \Sigma_{\min} P_{xi}, P_{yi} \qquad (2)$$

where:

P_{xi} is the relative frequency (in weight) of food category i in the stomach of species x (g);

P_{yi} is the corresponding frequency in species y, expressed as a percentage of the total weight of individuals of all food categories (g).

The index ranges from 0% (no overlap) to 100% (complete overlap). Trawlings were made repeatedly during particular seasons but the effectiveness of some of them was low due to lack of fish in the environment. Such trawls are included in tables but in further discussion we did not take them into consideration.

RESULTS

Total number of 176 individuals of sand goby, 70 individuals of common goby and 157 individuals of flounder were analyzed. The exact quantity and length of investigated gobies and flounder individuals, in particular seasons, are presented in Table 1.

Temporal changes of prey importance

In summer 2001, Calanoida and *Bathyporeia pilosa* were the most important prey in the diet of *Pomatoschistus minutus*. *B. pilosa* is still one of the major prey in the diet in autumn 2001 but Copepoda eggs were also an important segment of the diet. The sand goby mainly fed on *B. pilosa* in spring 2002 but in summer 2002 *Neomysis integer* was a much more important food item. Unidentified Mysidacea and *N. integer* were the most important prey in spring 2003. The significant food items in the sand goby diet in autumn 2003 were Harpacticoida and Insecta (Table 2).

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Table 1

Quantity (No) and length of analysed individuals of the sand goby, the common goby and the flounder [mm].

Sampling seasons	Species											
	P. minutus				*P. microps*				*P. flesus*			
	No.	mean	min.-max.	median	No.	mean	min.-max.	median	No.	mean	min.-max.	median
Summer 2001	49	39.85	30 – 52	39.0	1	-	35	-	4	47.25	30 – 85	37.0
Autumn 2001	87	41.96	32 – 63	41.0	17	34.94	26 – 42	37.0	8	50.75	35 – 70	48.0
Spring 2002	13	52.76	41 – 61	52.0	2	57.50	55 – 60	57.5	32	50.28	36 – 95	48.5
Summer 2002	2	54.50	51 – 58	54.5	3	46.66	40 – 55	45.0	11	59.72	18 – 94	70.0
Autumn 2002	-	-	-	-	-	-	-	-	8	67.25	40 – 95	63.5
Winter 2002	-	-	-	-	-	-	-	-	2	42.50	37 – 48	42.5
Spring 2003	20	50.10	39 – 65	49.5	6	50.00	48 – 53	49.0	41	48.73	34 – 67	50.0
Summer 2003	-	-	-	-	-	-	-	-	7	68.00	45 – 90	66.0
Autumn 2003	5	48.80	45 – 55	48.0	1	-	52	-	21	51.10	29 – 78	48.0
Autumn 2003 Chałupy[a]	-	-	-	-	40	23.80	19 – 30	23.0	23	44.39	36 – 72	42.0
total quantity of individuals	176				70				157			

[a]AUTUMN 2003 Chałupy – data in this row refer to samples from Chałupy station only

Table 2

Temporal changes of prey importance in *P. minutus* diet [%IRI] (‘undet.’ means that the prey was determined to order, ‘eggs other’ refer to eggs other than copepod eggs, ‘Copepoda eggs’ refer to eggs which were not in the egg sacks).

Prey item	Sampling seasons						
	Summer 2001	Autumn 2001	Spring 2002	Summer 2002	Spring 2003	Autumn 2003	Mean
Nematoda	0.02	0.09	0.00	1.53	0.12	0.00	**0.293**
Polychaeta undet.	0.11	0.00	0.00	0.00	6.82	0.00	**1.155**
Annelida undet.	0.00	0.00	0.00	1.53	1.16	0.00	**0.448**
Calanoida	65.40	0.52	0.00	3.08	0.29	0.00	**11.548**
Harpacticoida	0.69	7.56	0.08	0.00	0.00	56.34	**10.778**
Copepoda undet.	1.67	1.74	0.00	0.00	8.74	0.00	**2.025**
Copepoda eggs	7.08	52.40	0.00	0.00	10.45	0.00	**11.655**
N. integer	0.01	5.69	12.92	71.80	40.13	0.00	**21.758**
Mysidacea undet.	0.01	0.41	0.46	0.00	12.66	0.00	**2.257**
B. pilosa	16.19	23.11	85.14	22.06	0.00	0.00	**24.417**
Gammarus sp.	0.02	0.11	0.00	0.00	0.00	6.83	**1.160**
Amphipoda undet.	2.75	8.04	0.48	0.00	0.74	0.00	**14.377**
Chironomidae	3.11	0.00	0.00	0.00	0.00	0.00	**0.518**
Insecta undet.	0.04	0.02	0.00	0.00	0.66	36.84	**6.260**
P. minutus	2.18	0.03	0.00	0.00	0.00	0.00	**0.368**
Eggs other	0.07	0.01	0.00	0.00	17.44	0.00	**2.920**
No of stomachs	49	87	13	2	20	5	

Similarly, as for the sand goby, Calanoida were very significant in the common goby diet in summer 2001. *Pomatoschistus microps* food composition from autumn 2001 presented similarly dominant proportions of *B. pilosa* and Copepoda eggs IRI values as for *P. minutus* for the same season. In spring 2002, summer 2002 and spring 2003 *P. microps* mainly fed on *N. integer.* Its diet in spring 2003 was also composed of Insecta to a great extent. The common goby stomach content from autumn 2003 was completely dominated by unidentified Amphipoda. In autumn 2003 (Chałupy station) *Bosmina coregoni maritima* and Polychaeta occurred in the diet, which had not been previously recognized as a food source for this species. However, they were still only a minor group of prey when compared to the IRI values of Harpacticoida (Table 3).

Table 3

Temporal changes of prey importance in *P. microps* diet [%IRI] ('undet.' means that prey was determined to order, 'eggs other' refer to eggs other than copepod eggs, 'Copepoda eggs' refer to eggs which were not in the egg sacks).

Prey item	Sampling seasons							
	Summer 2001	Autumn 2001	Spring 2002	Summer 2002	Spring 2003	Autumn 2003	Autumn 2003 Chał.[a]	Mean
Nematoda	0.00	0.02	0.00	0.00	1.76	0.00	0.00	**0.254**
Polychaeta undet.	0.00	0.00	0.00	0.00	0.00	0.00	7.38	**1.054**
B. coregoni maritima	0.00	0.00	0.00	0.00	0.00	0.00	12.21	**1.744**
Calanoida	51.25	0.92	0.00	0.00	0.00	0.00	0.05	**7.460**
Harpacticoida	0.97	20.51	0.00	0.00	0.00	0.00	73.64	**13.589**
Copepoda eggs	0.00	40.80	0.00	0.00	0.00	0.00	0.12	**5.846**
N. integer	30.77	9.48	82.71	77.31	44.48	0.00	0.00	**34.964**
Mysidacea undet.	0.00	0.47	0.00	0.00	8.86	0.00	0.00	**1.333**
B. pilosa	0.00	25.80	17.29	7.03	0.00	0.00	1.23	**7.336**
Gammarus sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.08	**0.011**
Amphipoda undet.	16.05	1.98	0.00	0.00	0.00	100.00	0.23	**16.894**
Chironomidae	0.00	0.00	0.00	0.00	0.00	0.00	5.03	**0.719**
Insecta undet.	0.00	0.00	0.00	0.00	41.67	0.00	0.00	**5.953**
Pisces undet.	0.00	0.00	0.00	12.99	0.00	0.00	0.00	**1.856**
Eggs other	0.97	0.00	0.00	2.67	0.00	0.00	0.02	**0.523**
No of stomachs	1	17	2	3	6	1	40	

[a]AUTUMN 2003 Chałupy – data in this column refer to samples from Chałupy station only

Copepoda eggs and *B. pilosa* made up the diet of *Platichthys flesus* in summer 2001 but in the same season of the year 2002 *N. integer* was also prominent in the diet, and in 2003 *Nereis diversicolor* gained prominence. The Copepoda eggs were the most important food in flounder stomachs in autumn 2001, spring 2002, autumn 2002, winter 2002 and spring 2003. *N. integer* was an important component in the diet in autumn 2002 and spring 2003. The flounder fed on *P. minutus* only in September 2002. The high IRI values of

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Harpacticoida were calculated for flounder stomachs only in spring 2003. In autumn 2003 at Sopot and Chałupy stations unidentified Polychaeta were the most important food for flounder (Table 4).

The major food during all three years of study for *P. minutus* were *B. pilosa*, *N. integer*. For *P. microps* the major foods were *N. integer*, Amphipoda unidentified and Harpacticoida, and for *P. flesus* the major foods were Copepoda eggs, Polychaeta and *B. pilosa*.

Niche comparisons

The prey items which most distinguish the flounder diet composition from Chałupy and Sopot stations (autumn 2003) are Chironomidae, Polychaeta and Harpacticoida (Fig. 2). Polychaeta, *Bathyporeia pilosa* and Harpacticoida were more important for the flounder individuals feeding in shallow waters near Sopot than for individuals feeding in waters near Chałupy. Values of relative importance index of Copepoda eggs are very close for both stations (Table 4).

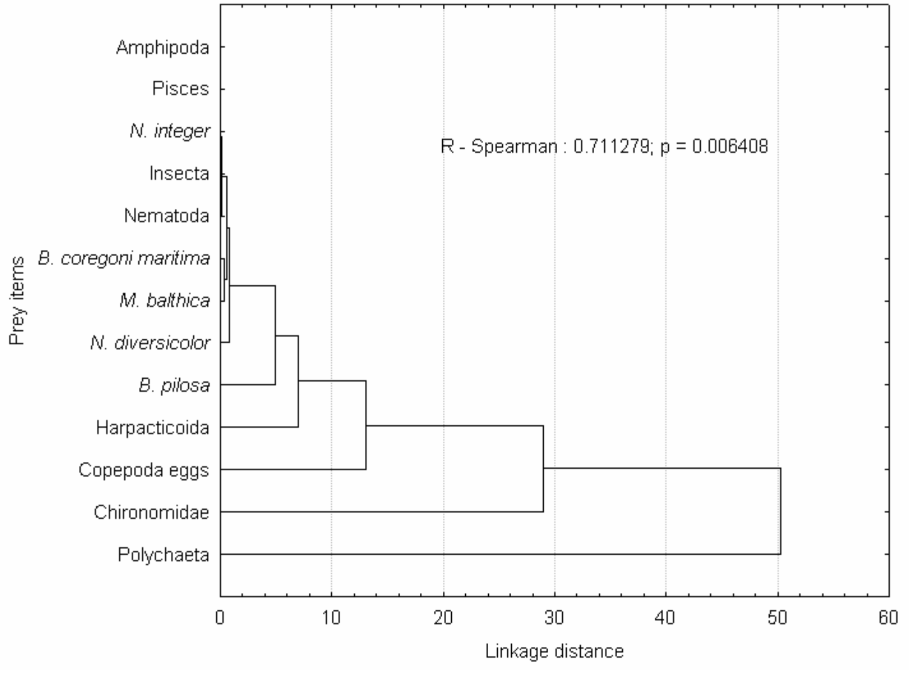

Fig. 2. Comparison of flounder trophic niches at Chałupy and Sopot stations (autumn 2003).

Table 4

Temporal changes of prey importance in *P. flesus* diet [%IRI] ('undet.' means that prey was determined to order, 'eggs other' refer to eggs other than copepod eggs, 'Copepoda eggs' refer to eggs which were not in the egg sacks).

	Sampling seasons										
Prey item	Summer 2001	Autumn 2001	Spring 2002	Summer 2002	Autumn 2002	Winter 2002	Spring 2003	Summer 2003	Autumn 2003	Autumn 2003 chał.[a]	Mean
Nematoda	0.00	0.05	0.00	0.02	0.00	0.00	0.03	0.27	0.08	0.00	**0.045**
N. diversicolor	0.00	0.00	3.75	0.00	2.65	0.00	1.15	28.63	0.00	0.81	**3.699**
Polychaeta undet.	4.86	4.65	0.42	1.82	0.00	0.00	14.13	0.00	61.48	39.52	**12.688**
Annelida undet.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.27	0.00	0.00	**0.027**
B. coregoni maritima	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.84	0.31	**0.115**
Calanoida	0.35	0.00	0.00	0.02	0.00	0.00	0.00	2.96	0.00	0.00	**0.333**
Cyclopoida	0.23	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	**0.025**
Harpacticoida	0.00	10.07	2.50	6.71	0.00	0.00	25.52	0.00	12.34	3.25	**6.039**
Copepoda eggs	31.75	32.74	69.05	59.41	66.61	87.38	28.84	34.45	17.47	15.30	**44.300**
N. integer	0.00	18.74	1.75	18.45	22.61	0.00	28.21	0.93	0.00	0.05	**9.074**
Mysidacea undet.	0.00	0.06	0.00	0.00	0.00	12.62	0.00	0.00	0.00	0.00	**1.268**
B. pilosa	62.58	0.84	22.47	13.50	0.00	0.00	2.01	29.19	5.77	0.99	**13.735**
Amphipoda undet.	0.00	0.00	0.04	0.00	0.00	0.00	0.04	0.00	0.00	0.04	**0.012**
Chironomidae	0.00	0.20	0.00	0.00	0.00	0.00	0.03	0.27	1.19	39.31	**4.100**
Insecta undet.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	**0.002**
M. balthica	0.00	10.74	0.00	0.00	0.00	0.00	0.00	0.00	0.69	0.00	**1.143**
P. minutus	0.00	0.00	0.00	0.00	8.08	0.00	0.00	0.00	0.00	0.00	**0.808**
Pisces undet.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.76	0.00	0.04	**0.280**
Eggs other	0.00	21.87	0.00	0.00	0.05	0.00	0.01	0.28	0.00	0.00	**2.221**
No of stomachs	4	8	32	11	8	2	41	7	21	23	

[a]AUTUMN 2003 Chałupy – data in this column refer to samples from Chałupy station only

Diet similarity

A significant overlap in food sources between two goby species is represented by values of percentage overlap index in summer 2002. The results also indicate that the *Pomatoschistus minutus* trophic niche has a high overlap with *Platichthys flesus* in summer 2001, summer 2002 and spring 2003. It also appears that *Pomatoschistus microps* and *P. flesus* took similar weight proportion of available food in autumn 2003 (Chałupy station) (Fig. 3, Table 5).

Average diet similarity for the principal food items between each two fish species remains constant during the whole investigation time (Fig. 4).

Table 5

Seasonal diet overlap between investigated fish species.

Fish species	Sampling seasons					
	Summer 2001	Autumn 2001	Spring 2002	Summer 2002	Spring 2003	Autumn 2003[a]
P. minutus / P. microps	14.46%	54.30%	43.00%	64.81%	39.38%	0.00%
P. minutus / P. flesus	74.71%	16.86%	49.01%	60.21%	79.38%	0.00%
P. microps / P. flesus	0.02%	24.86%	36.11%	47.52%	33.27%	68.72%

[a]AUTUMN 2003 Chałupy – data in this column refer to samples from Chałupy station only

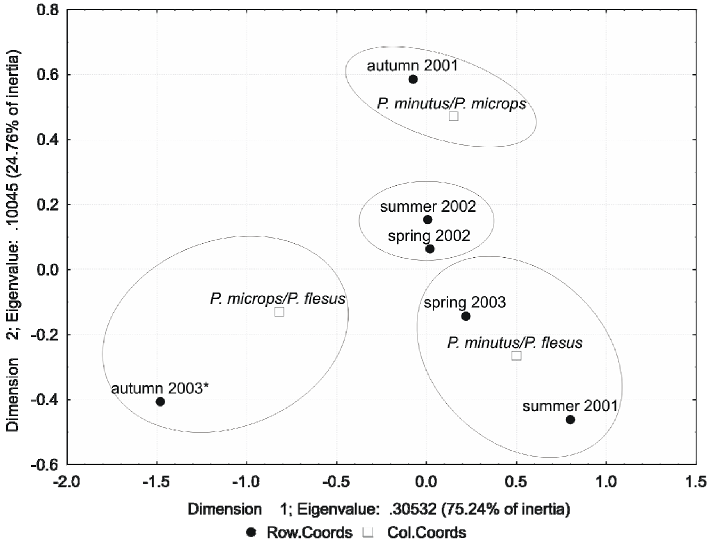

Fig. 3. Correspondence analysis of seasonal diet similarity (food-niche overlap) between investigated fishes (input table (Rows × Columns): 3 × 6; standardization: row and column profiles)
*autumn 2003 - data refer to samples from Chałupy station only

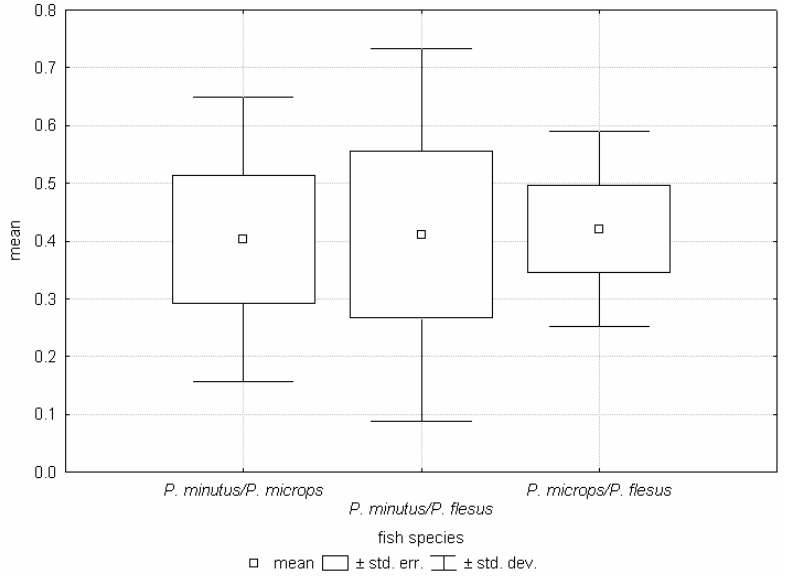

Fig. 4. Mean values of average diet similarity (food-niche overlap) between investigated fishes during the whole investigation time.

DISCUSSION

Larger prey, for example amphipods undet., *Bathyporeia pilosa* or *Neomysis integer*, were significant food items for *Pomatoschistus minutus* and *Pomatoschistus microps* during the whole investigation. In case of lack of those prey items in gobies' stomachs, essential prey for *P. microps* were harpacticoids. An effective change towards feeding on smaller food objects is probably connected with the different lengths of the two gobies at the time of migration to the coastal zone. Individuals of the sand goby are longer than individuals of the common goby (Pihl 1985). The same fact was observed in the currrent study.

The flounder is strongly selective in its food choice (Mulicki 1947). Samples investigated by Mulicki mainly come from autumn and spring. The frequent food components were *N. integer*, *Nereis diversicolor* and *Gammarus* sp. Only Polychaeta were equally important in stomachs from autumn 2003. *N. integer* proved an insignificant percentage of total food items and *Gammarus* sp. was not found at all. The young flounders prefered to feed on worms and crustaceans than on bivalves with hard calcium shells (Ostrowski

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1997). As stated elsewhere in the present study, the minor prey was not Polychaeta but Chironomidae. Molluscs were more often found in older flounder stomachs and the shells were crumbled into pieces which indicates that the flounder manages well with this kind of prey.

Food selection of gobies depends on several factors, e.g. availability of the prey which is mainly determined by its density, visibility and mobility (Zander 1979). *N. integer* is a very important food item for the sand goby, as observed by Aarnio and Bonsdorff (1993). This is probably due to the behaviour of this species. It is a free-swimming species and is more easily observed by *P. minutus,* which is a visual predator (Edlund, Magnhagen 1981), than by species living buried in the sediment.

The experiments conducted by Magnhagen and Wiederholm (1982) and by Wiederholm (1987) showed that *P. minutus* is a generalist in its habitat selection, so it chooses open and vegetated areas in equal proportion, while *P. microps* prefers open areas. According to this, the coexistence of two gobies in the same area, in the same part of the Gulf of Gdańsk, may increase the frequency of social interactions between them and encourage the separation of food resources. In consequence being in close proximity to one another has more influence on food choice than food availability and foraging time as predicted by Schoener (1974). The common goby occupies the shallowest part of the eulittoral zone, while the sand goby is found somewhat deeper in this zone (Ławacz 1965, Gibson 1973), which does not mean that both gobies do not live together. The evidence for their coexistence in shallow water is the fact that they are caught together in the same trawl. Probably larger sand goby pressurizes smaller common goby too much and it has to live in a less prey-abundant but safer environment. Such size-dependant habitat segregation of gobies has already been observed along the Baltic coast of the west part of Sweden (Pihl, Rosenberg 1982). It has a direct influence on the kind of food eaten. Chironomids and insects are found in high densities on the water-land boundary and they are three times more abundant in the food of *P. microps* than *P. minutus.* The occurrence of *P. microps* so close the shoreline can be favourable for it because of the low number of other fish and consequently lower competition for prey.

Incidences of the investigated species feeding upon eggs of their own species has not been observed, however, some predation by *P. minutus* on their young individuals occurred which was also previously noted by Hesthagen (1977). It is caused by the occurrence of both young and adult fish in the same area. *P. microps* preyed upon unidentified fish and in low quantity. Young individuals of *P. minutus* were found exclusively in the flounders' stomachs. This is due to the general length difference between these two species. Larger flounder individuals are able to consume smaller sand goby, e.g. in autumn.

The structure of the shallow-water community is partially regulated by the environment which is characterized by large fluctuations in physical variables. The fact that the sand goby and the common goby differ in their prey choice does not mean that the food supply is the differentiating factor. Magnhagen and Wiederholm (1982) concluded that habitat is more important than food supply as a segregating niche dimension, because of the decreased frequency of social interactions between the two species of gobies. The results of the current investigation also show that both gobies do not coexist together with similar abundance. At Sopot station there were more individuals of the sand goby but at Chałupy station the common goby was found more often, which is probably a consequence of different habitat choices. *P. minutus* is often found both in vegetated and open areas, whereas *P. microps* prefers open areas (Wiederholm 1987). However, for consumer populations, the dependence upon other organisms for food probably is more important as regulator than the physical environment, which can be avoided when unfavourable (Evans, Tallmark 1985). At Sopot station the dominant meiofaunal group of organisms was Gastrotricha (62.3%) (Kotwicki 2004), however none of three investigated fish fed on it. Nematoda and Harpacticoida were both more common food sources. All three fish species fed on significant amounts of Harpacticoida in spite of the fact that Nematoda were more abundant in the environment. In the first centimeters of sediment from Sopot station Harpacticoida are rare, whereas the highest number of Nematoda is found between zero and five centimeters (Kotwicki 2004). Active selection for Harpacticoida from sediment cannot be explained because fish utilize only a few upper centimeters of sediment (Gee 1987). Rapid digestion of nematodes cannot be the cause for their rarer presence in fish stomachs, because their chitinous integument does not seem to be destroyed by digestive processes (own observation). The bulk of individuals of this order were isolated from stomachs in good condition and easily identified. Probably, Nematoda pass intact through fish intestine as already reported by McIntyre in 1969 for flatfish (Alheit, Scheibel 1982).

The low number of Harpacticoida in sediment does not necessarily mean that they are unavailable for epifauna. Inshore current systems and wave action determine the availability of these organisms as potential prey items (Lasiak, McLachlan 1987). So, in the coastal zone, the dynamic of the water and fish activity should make meiofauna more accessible for fish, especially from deeper parts of the sediment. However, Palmer's work from 1988 shows that even when meiofauna organisms are dense in the water column their consumption is low. He explains this phenomenon as an apparent higher availability of prey because the factors mentioned above do not affect meiofaunal assemblage more than foraging activity of fish.

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P. microps and *P. flesus* chose to feed on Copepoda individuals from the suborder Harpacticoida more often than individuals from the suborder Calanoida. However, *P. minutus* fed on both suborders in equal proportion. The higher significance of larger food items in *P. minutus* stomachs are probably due to different digestion rates of food particles of different size. Larger Calanoida retain in the stomach for a longer period than smaller Harpacticoida and the former are more effectively digested (Berg 1979). Besides, *P. minutus* could have been utilizing different, higher parts of the water column. That may be why it chose planktonic prey rather than benthic ones. Another important cause may be daily feeding migration of fish. The fish stomachs contained organisms inhabiting the coastal zone to a large extent but also included ones from the deeper part of the water column in small amounts.

The availability of preferable food items does not always determine the composition of fish diet. A partial influence on the diet is the presence of other fish. When comparing trophic niches of Chałupy and Sopot stations, the first one is rich in Polychaeta and poor in Chironomidae (Kotwicki 1997). It is also known that under the influence of some contaminants, Polychaeta may become the dominant group of organisms in the environment and consequently they are more accessible for demersal-feeding fish (Hesthagen 1977). Nevertheless, the flounder in autumn 2003 at Chałupy station fed on this class less frequently than in the same month at Sopot station. Explanations could be various, e.g. the change of dominant species among macrozoobenthos (Kotwicki 1997) or other species pressure. At Sopot station in autumn 2003 the sand goby was also present. Harpacticoida and Calanoida held equal importance in the diet, thereby decreasing the competition over benthic harpacticoids. At Chałupy station *P. flesus* coexisted with *P. microps* for which Harpacticoida are also an important food item. Increased competition made the IRI index for Harpacticoida four times lower than at Sopot station. Chironomidae were more important for the flounder than Polychaeta, which have a higher biomass in the environment. Probably the loss of high energy food such as Harpacticoida caused the flounder to choose to feed on the more energy-dense Chironomidae rather than on Polychaeta.

It is suggested, e.g. by Dill (1983), that many fish broaden their diet to consist of less-preferred prey and in consequence hunger increases. Diet broadening is an adaptive behaviour only if energy losses caused by foraging different kinds of food are not higher than the benefit gained from eating those foods. Behavioral changes are more marked for the prey which has not already been included in the diet or consisted of only a small part of it. Moreover, fish possess the ability to alter their behaviour in this flexible way in response to changing factors such as threat of competition and risk of predation (Dill 1983). Such adaptive behaviour can be seen for the flounder. High activity increases vulnerability to predation, so narrowing the range of prey and decreased foraging activity do not have to be a consequence of low food availability, but may be viewed as an adaptive response to predation risk.

Generally *P. minutus* and *P. microps* are not selective in their food choices when they do not occur in the same zone together and the abundance of prey is high. When the number of food organisms decreases both fish species consume the same, more available kind of prey (Edlund, Magnhagen 1981). The rate of consumption of both gobies is relatively high (Złoch et al. 2005), indicating high food density at Sopot and Chałupy stations. According to this, both gobies react in a similar way to that described by Edlund and Magnhagen (1981). In autumn 2003 at Chałupy station, when the common goby was found without the sand goby, it fed on the same food (Harpacticoida: %IRI = 70%) as the sand goby did during a similar period at Sopot station. This fact means that in the presence of the sand goby, the common goby narrowed its food niche by restricting its diet to *N. integer* from spring 2002 to spring 2003 and to Amphipoda undet. in summer 2001 and in autumn 2003 (value of index of relative importance) while being suppressed by the larger sand goby. *N. integer* was also consumed to a certain extent by *P. minutus*, which suggests that these two species may compete over this food resource but despite this both gobies survive in coexistence even if *P. microps* eats less than the socially dominating *P. minutus* (the rate of consumption is lower) (Złoch et al. 2005).

Generally, the degree of food niche overlap decreases with increasing difference in fish body size between two gobies, because smaller organisms mainly feed on meiofauna and larger ones on macrofauna. The largest niche overlap between two goby species occurred in autumn 2001 and summer 2002. Despite the fact that individuals of *P. microps* are smaller than those of *P. minutus*, the size of the two gobies are not considerably different in these months. The low value of percentage overlap index is caused rather by a low number of investigated fish than differences in total length of the individuals. In spite of greater size differences between *P. minutus* and *P. flesus,* their trophic niches overlap more often than between gobies, but the magnitude of the highest values of the percentage food overlap index is not as high as for the common goby and the sand goby. Also, the increased value of the overlap index during the summer season can be partly caused by the higher density of investigated fish species in the shallow water zone. As well, along with high differences in fish size, high overlap index is best shown for *P. microps* and *P. flesus* in autumn 2003 and summer 2002. In the other seasons food niches of fish did not overlap on as large a scale despite the fact that fish lengths did not differ significantly. The mean overlap value for *Pomatoschistus* sp. were not as high as in, e.g. Pihl's study (1985), – about 50%, probably due to large differences in the quantity of analyzed stomachs (higher quantity in the present

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study). The similarity of the diet between fish may be reduced by seasonal variation in the proportion of actual food intake, foraging behaviour, prey size and its abundance in the environment (Nasir 2001).

The competition between *P. microps* and *P. minutus* has already been confirmed in the laboratory, e.g. by Magnhagen and Wiederholm (1982), and it increases in summer when the depletion of food resources, which may be caused by pressure of young organisms (not only fish), occurs. This phenomenon was not confirmed by the current study, since during other seasons when the sample of stomachs was big enough, the competition between both gobies was significant. A slight decrease in food niche overlap in the case of the coexistence of gobies in spring 2003 is probably due to increasing competition for *N. integer* and, in summer 2001, for Calanoida and to the search for new, additional food supplies. It should be noted that it is not sufficient to show differences in food selection between two species living together to explain their coexistence. Social dominance, often associated with a larger body size of one of the investigated species, may exclude another species from its habitat, even though it utilizes an unimportant 'food refuge' for the other fish (Edlund, Magnhagen 1981).

According to Kislaliogiu, Gibson (1977) values of food niche overlap exceeding 60% are significant. Relatively low and similar values of percentage overlap index for all investigated fish species during the whole study period, suggest that shallow, soft bottoms of the Gulf of Gdańsk provide a good food supply that neither limits their growth nor produces severe competition between them, even though their food niches are much the same. The high reproduction and short life cycle of potential food organisms are the factors which prevent their population from experiencing extensive predation. So, in consequence, their abundance cannot regulate the number of fish inhabiting shallow, sandy bottomed waters (Evans 1983) and competition for them does not exert an important impact on structuring the fish assemblage.

CONCLUSION

The high importance of *Neomysis integer,* which exclusively lives in coastal waters, in the diet of all three investigated fish species, indicates that they utilize this zone as a feeding ground. A question of the importance of eulittoral habitat use has also led to the conclusion that fish are very flexible in their food choices and use different food sources (the distribution of *Bathyporeia pilosa*, Harpacticoida and *Nereis diversicolor* is not confined to shallow areas). The results suggest that the examined fish are macrobenthic feeders and their trophic niches overlap in a similar, insignificant way.

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