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Diet of the twaite shad *Alosa fallax* (Lacépède, 1803) (Clupeidae) in the Gulf of Gdansk, the Baltic Sea

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Abstract

Twaite shad *Alosa fallax* (12 – 48 cm total length) from the Gulf of Gdansk feed on Mysids: *Mysis mixta*, *Neomysis integer*, and fish: *Sprattus sprattus*, *Osmerus eperlanus*, and *Pomatoschistus* sp.. In the stomachs of *A. fallax* there also occur *Hydobia* sp., Diptera and small stones, particles of wood and plastic. The food of inshore twaite shad measured from 12 to 21 cm centered on *M. mixta*. Fish are the main prey for *A. fallax* from the class length 22 – 31 cm from the Vistula River mouth and for all shads longer than 32 cm.

INTRODUCTION

According to Kottelat and Freyhof (2007), the twaite shad *Alosa fallax* (Lacépède, 1803) occurs along the Atlantic coast from Morocco to Ireland and Scotland, in the North Sea to Bergen, including the southern Baltic Sea, in the northern Mediterranean, and occasionally in the northern Black Sea reaching Crimea. Aprahamian et al. (2003), based on the distinction of the *Alosa fallax* subspecies by Quignard and Douchement (1991), described the distribution of Atlantic anadromous twaite shad as an area from Iceland to Morocco including the Baltic Sea.

Up to 300 tons per year of twaite shad were caught in the rivers of German fisheries at the beginning of the 20th century (Popiel 1962). The fishery statistics from 1889-1938 showed that 20 to 56.4 tons per year of *A. fallax* were caught in the Vistula Lagoon (Bartel et al. 1996), and from 5.3 to 185.1 tons were caught per year in the Szczecin Lagoon in the years 1889-1920 (Bartel et al. 1998). After the Second World War the number of described species decreased distinctly in the Baltic Sea region. According to Pęczalska (1973), in the years 1953 and 1955 numerous migrations of *A. fallax* to the Szczecin Lagoon were still observed, followed by successful spawning. Considering the distribution of the allis shad *Alosa alosa* (Baglinie et al. 2003), some juvenile twaite shad may have been recorded by Elwertowski (1957) as a by-catch of the commercial sprat fishery both in subdivisions 25 and 26 ICES in the early 1950s.

Since that time twaite shad has disappeared from the Baltic Sea fishing grounds used by the Polish fishery (Pęczalska 1973). After a long absence lasting until the mid-1990s, the *A. fallax* population has been increasing in Polish (Skóra 1996; Wilkońska, Garbacik-Wesołowska 1996; Więcaszek,

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Krzykawski 1999; Szulc, Domagała 1999; Hesse 2000a,b,c; Skóra 2000, 2001; Szulc et al. 2001; Draganik et al. 2006, 2007; Domagała, Szulc 2007), Lithuanian (Maksimov, Toliusis 1998; Svagzdys 1999; Repecka 2001; Zolubas, Toliusis 2001; Repecka 2003; Maksimov 2004; Bacevičius 2007a; Zolubas, Piščikas 2007), Russian (Guschin, Tverdokhle 2009) and German (Thiel et al. 2007, 2008) Baltic waters.

Twaite shad was included in the Red Data Books of Animals of both Lithuania (Repecka 1992) and Poland (Skóra 2001). Since the population has increased to a commercially exploitable level in Lithuanian waters, *A. fallax* has been excluded from the Red List of Lithuania (Zolubas, Piščikas 2007; Kesminas, Svecevičius 2008). It has been strictly protected by Polish law since 1995 (Skóra 1996). However, each year *A. fallax* derived from illegal catches can be found in local fish markets.

Observations on the feeding of twaite shad larvae and/or juveniles have been published by Aprahamian (1988, 1989), Oesmann, Thiel (2001), Bacevičius (2007b), and Nunn et al. (2008). Studies on the diet of sub-adult and adult *A. fallax* during their marine life phase or pre-, post- and spawning migration were carried out by Aprahamian (1989), Assis et al. (1992), Taverny, Elie (2001), Doherty, McCarthy (2002), Maitland, Lyle (2005), Schulze, Schirmer (2006) and Bacevičius (2007b). Information about food items are also provided, for example, by Svetovidov (1952) and Wheeler (1969). Most studies, with the exception of Bacevičius (2007b), concerned populations of twaite shad from the Atlantic Ocean coast and revealed that *A. fallax* feed on various small fishes and crustaceans at sea.

The aim of this study was to gain knowledge about the species composition of the twaite shad diet in the southern Baltic Proper.

MATERIALS AND METHODS

Material was collected from December 1999 to May 2002. A total of 247 twaite shads were examined. The shads were received from professional fishermen operating in the Gulf of Gdansk. The fish were caught in two different types of habitats. Some were caught near the Vistula River mouth by fishery boats that used gill nets and the rest was caught from the inshore area of the Gulf of Gdansk both by fishery vessels that used the bottom trawls and those using gill nets (Fig. 1). A complete listing of dates, types of fishing gear, and the number of specimens collected are presented in Table 1.

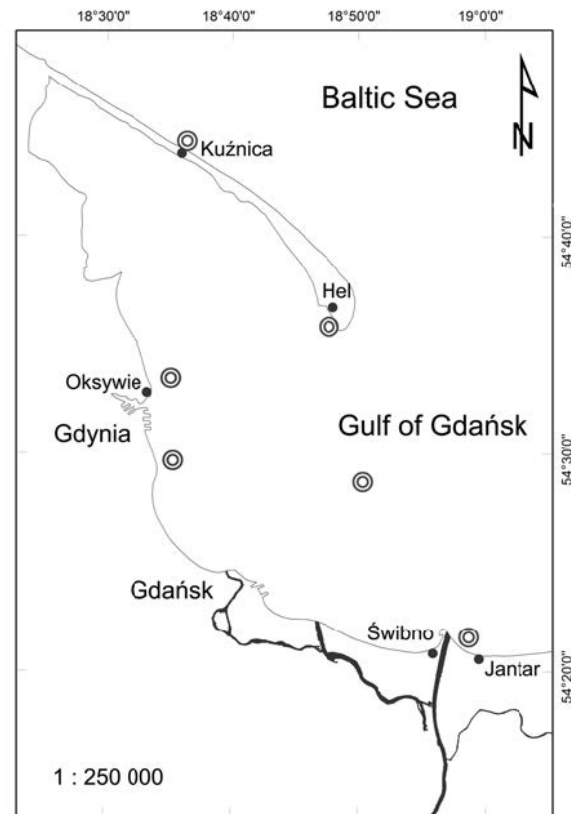


Fig. 1. The fishing ground of analyzed fish.

Table 1

Date of catch and number of collected twaite shads.

Year	Month	Fish number	Fishing gear	Type of habitats	Fishery harbour
1999	X-XI	2	gill nets ¹	the Gulf of Gdansk	Oksywie
1999	XII	100	bottom trawl ²	the Gulf of Gdansk	Kuźnica
2000	VIII	3	gill nets ¹	the Vistula River mouth	Jantar
2000	IX-XI	17	gill nets ¹	the Vistula River mouth	Jantar
2001	I	73	unknown	the Gulf of Gdansk	unknown
2001	V	3	gill nets ¹	the Vistula River mouth	Jantar
2001	VI	1	gill nets ¹	the Vistula River mouth	Jantar
2001	VII	3	gill nets ¹	the Vistula River mouth	Jantar
2001	VIII	1	gill nets ¹	the Vistula River mouth	Świbno
2001	VIII	5	gill nets ¹	the Vistula River mouth	Jantar
2001	?	5	gill nets ¹	the Gulf of Gdansk	Oksywie
2001	IX	1	gill nets ¹	the Vistula River mouth	Świbno
2001	IX	3	gill nets ¹	the Gulf of Gdansk	Oksywie
2001	X	4	gill nets ¹	the Gulf of Gdansk	Oksywie
2001	IX-XI	2	gill nets ¹	the Gulf of Gdansk	Oksywie
2001	XII	1	gill nets ¹	the Gulf of Gdansk	Oksywie
2001	?	4	gill nets ¹	the Vistula River mouth	Jantar
2002	IV	2	gill nets ²	the Gulf of Gdansk	Hel, Kuźnica
2002	V	8	gill nets ²	the Gulf of Gdansk	Hel

¹ - mesh 65 mm, net thickness 0.25 mm,

² - unknown

Fresh or frozen twaite shads were received, and stored frozen. Total fish length was measured in millimetres.

Based on the length–frequency distribution in 1 cm classes of collected *A. fallax*, the fish were divided into 3 length–class groups: from 12 to 21 cm

(the small shads), from 22 to 31 cm (the medium shads), and longer than 32 cm (the large shads). Because of different types of fish habitats, two subgroups in the second and in the third length-classes were formed, in order to facilitate the study of the relationship between *A. fallax* length and diet.

At the laboratory, stomachs were cut out of the thawed fish and preserved in a 4% buffered formaldehyde solution. The degree of stomach fullness was rated on a scale of 0 to IV based on visual estimation, with 0 being empty and IV being full. The contents of 205 stomachs were analysed for quality and quantity. The diet was identified by the food items found in the stomachs, which were identified to the lowest possible taxonomic level. The food compounds were weighed with a 0.01 g accuracy. The relative numerical abundance and weight, and the frequency of occurrence of each food item were calculated and combined into the Index of Relative Importance (I.R.I.) (Pinkas et al. 1971), where the weight contribution of each prey was used in place of volume measures. The frequency of occurrence (F) was also used to determine 3 prey categories: preferential ($F > 50$), secondary ($10 < F < 50$), and occasional ($F < 10$) [Assis et al. (1992) from Albertini – Berhaut (1973)]. The empty stomachs and those containing only unrecognized heavily digested animal tissue were not taken into consideration when calculating the relative numerical abundance, weight, frequency of occurrence, and I.R.I. Fish scales were excluded from fish as one of the main categories of food compound to prevent overestimation of its role in the diet.

RESULTS

The investigated twaite shads measured from 122 to 480 mm in total length. Bimodal length-frequency distribution (in 1 cm classes) was observed. Fish were most abundant in two length-classes: 15 cm (16.5%) and 27 cm (12.1%). The length-frequency distributions in 1 cm classes were similar to the Gauss distribution taking into account separately the length-class groups: from 12 to 21 cm (40.3% of fish), from 22 to 31 cm (50.4% of fish), and longer than 32 cm (11.7% of fish) (Fig. 2).

Fish with empty stomachs (0) dominated among the analysed individuals (32.2%) (Fig. 3). Class II stomachs categorized 15.1% of the fish. The percentage of fish with completely full stomachs (IV) was 22.4%. The specimens with intermediate degrees of stomach fullness (I and III) amounted to 30.2%.

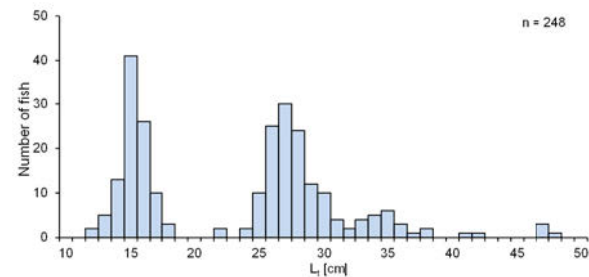


Fig. 2. Length-frequency distribution of analyzed *A. fallax*.

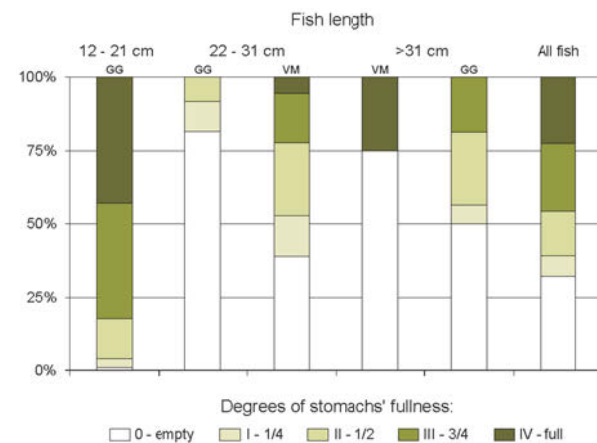


Fig. 3. The degrees of stomach fullness distribution in the length-classes of twaite shads. Abbreviations used: GG – the Gulf of Gdansk, VM – the Vistula River mouth.

The majority of small shad stomachs were categorized as class III and IV (82.0%). The empty stomachs amounted to only 1.0%.

Less than half the investigated shads from the length-class group 22 to 31 cm from the Vistula River mouth had empty stomachs (38.9%). Half-full stomachs occurred in 25.0% of specimens, and 5.6% of the fish had completely full stomachs. Among the medium shads from the inshore area of the Gulf of Gdansk, most had empty stomachs (81.6%). Only 10.2% of specimens had half full stomachs. No specimens with class III or IV stomachs were observed at all.

Half of the stomachs of the largest shad from the inshore area of the Gulf of Gdansk belonged to classes 0, I and II degrees of stomach fullness.

Seven food items were observed in the diet of *A. fallax* from the Gulf of Gdansk. The most important were crustaceans (*Mysis mixta* and *Neomysis integer*) and fish (*Sprattus sprattus*, *Osmerus eperlanus*, *Pomatoschistus* sp.). Mollusks (*Hydrobia* sp.), insects (Diptera), fish scales, small stones, pieces of wood, and incidental

remains of plants and plastic were also found in shad stomachs.

The preferential food items for the first length-class group of *A. fallax* was mysids. These crustaceans had the largest relative numerical abundance (93.5%) and weight (97.8%). The most common species was *M. mixta* (number 79.7%, biomass 84.8%). The occasional food items consisted of small fish (*Pomatoschistus* sp.) and snails (*Hydrobia* sp.). The participations of these food items in the relative numerical abundance was not higher than 0.8%, and their relative weight was lower than 1.8% (Table 2, Fig. 4).

The diet of specimens from the length-class group of 22 to 31 cm was dissimilar. In the stomachs of subgroups of *A. fallax* caught in the inshore area of the Gulf of Gdansk, the items with highest relative numerical abundances were small stones, wood (39.4%), and fish scales (31.6%). Their shares in the relative weight were 5.3% and 0.5%. The mysids (preferential food items) dominated in terms of relative weight (82.0%), whereas the relative numerical abundance amounted to 25.0%. The occasional items - the fish - in the diet were of no significance: 0.2% in the relative numerical abundance and 1.0% in the relative weight.

Twaite shad from the vicinity of the Vistula River mouth ate many of the same foods but in different proportions. No mysids were found and fish were the dominant food items, amounting to 83.6% of the relative numerical abundance and 96.4% of the relative weight. The relative numerical

abundance of Diptera (3.4%), the remains of plants (1.7%), small stones, wood (6.8%), and plastic (3.4%) totalled 16.4% together. None of the compounds mentioned were higher than 1.0% when the diet was analysed in terms of relative weight.

The fish were also undisputedly the preferential food items for the large *A. fallax* (the length-class group of shads longer than 32 cm). *M. mixta* and *N. integer*, in the largest shads's diet from the inshore area of the Gulf of Gdansk, amounted to 6.7% in terms of relative numerical abundance and 0.1% in terms of relative weight. Without unrecognized heavily digested biomass (12.6% of the total biomass), the other food items were not higher than 0.1% of relative weight.

The index of relative importance (I.R.I.) for mysids decreases, as the length of twaite shads increases, from 19,130 to 88 for shads in the inshore area of the Gulf of Gdansk. The opposite trend was observed for fish. The I.R.I. (without fish scales as a separate compound) in the case of small and medium twaite shads increases rapidly from 8.0 and 2.0, respectively, up to an I.R.I. 11,910 for specimens exceeding a length of 32 cm. Both medium and large twaite shads from the Vistula River mouth had I.R.I. values of over 16,600. It was observed, that in the diet of large *A. fallax* (longer than 32 cm), fish from the family Clupeidae dominated, with the most significant being sprat *S. sprattus*. *Pomatoschistus* sp. occurred in the diet of all 3 length-class groups (I.R.I. values were 8, 2, and 17, respectively) and it was the only fish species found in the stomachs of *A. fallax*

Table 2

Percent composition of the diet of *A. fallax* by the length and the type of habitat.

Food composition	Length-classes groups																								
	From 12 to 21 cm (the small shads)					From 22 to 31 cm (the medium shads)										Longer than 32 cm (the large shads)									
	N = 100, the Gulf of Gdansk					N = 49, the Gulf of Gdansk					N = 36, the Vistula River mouth					N = 16, the Gulf of Gdansk					N = 4, the Vistula River mouth				
	n.	w.	F	c	I.R.I.	n.	w.	F	c	I.R.I.	n.	w.	F	c	I.R.I.	n.	w.	F	c	I.R.I.	n.	w.	F	c	I.R.I.
MYSIDS	93.5	97.8	100.0	p	19,130	25.0	82.0	87.8	p	9,395	—	—	—	—	—	6.7	0.1	13.0	p	88	—	—	—	—	—
M. mixta	79.7	84.6	99.0	p	16,269	25.0	38.3	42.9	s	2,712	—	—	—	—	—	2.2	0.1	6.3	o	14	—	—	—	—	—
N. integer	13.8	2.8	59.0	p	981	—	—	—	—	—	—	—	—	—	—	4.4	0.1	12.5	s	56	—	—	—	—	—
Mysidacea	—	10.4	82.0	p	1,035	—	43.7	67.3	p	2,946	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
FISH*	0.3	1.7	4.0	s	8	0.2	1.0	2.0	o	2	83.6	96.4	88.9	p	16,002	59.9	87.1	81.3	p	11,910	77.0	93.4	100.0	p	17,040
S. sprattus	—	—	—	—	—	—	—	—	—	—	19.8	35.0	41.7	s	2,281	28.9	59.1	43.8	s	3,852	23.1	14.5	25.0	s	940
Clupeidae	—	—	—	—	—	—	—	—	—	—	18.6	17.4	27.8	s	1,001	4.4	4.7	12.5	s	114	—	—	—	—	—
O. eperlanus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7.7	27.5	25.0	s	881
Pomatoschistus sp.	0.3	1.7	4.0	o	8	—	—	—	—	—	0.6	0.3	2.8	o	2	2.2	0.4	6.3	o	17	—	—	—	—	—
Pisces	—	—	—	—	—	0.2	1.0	2.0	o	2	44.6	43.7	72.2	p	6,383	24.4	22.9	62.5	p	2,957	46.2	51.4	100.0	p	9,759
fish scales	2.3	<0.1	14.0	s	84	31.6	0.5	55.1	s	1,771	1.1	<0.1	5.6	o	6	28.9	<0.1	12.5	s	361	—	<0.1	25.0	s	—
OTHERS	3.9	0.5	35.0	s	155	43.2	6.0	69.4	p	3,414	15.3	0.8	25.0	s	402	4.4	0.1	6.3	o	28	23.1	<0.1	25.0	s	579
Hydrobia sp.	0.5	<0.1	5.0	o	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	23.1	<0.1	25.0	s	579
Diptera	—	—	—	—	—	—	—	—	—	—	3.4	0.3	11.1	s	41	—	—	—	—	—	—	—	—	—	—
plant material	—	—	—	—	—	3.0	0.3	36.7	s	119	1.7	<0.1	8.3	o	14	—	—	—	—	—	—	—	—	—	—
stones, wood	3.3	0.5	31.0	s	117	39.4	5.3	61.2	p	2,733	6.8	0.3	16.7	s	119	4.4	0.1	6.3	o	28	—	—	—	—	—
plastic	0.1	<0.1	1.0	o	9	0.8	0.4	8.2	o	10	3.4	0.1	11.1	o	39	—	—	—	—	—	—	—	—	—	—
unknown biomass	—	—	—	—	—	10.6	—	—	—	—	2.9	—	—	—	—	—	12.6	—	—	—	—	6.4	—	—	—

N – number, n – composition by number, w – composition by weight, F – frequency of abundance (percent of stomachs with prey), I.R.I. – index of relative importance, c – prey category: p – preferential, S – secondary, O – occasional, * – fish scales excluded

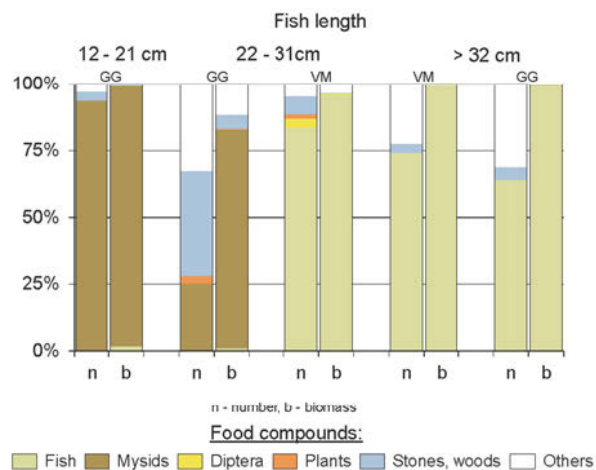


Fig. 4. The relative numerical abundance and weight of food items of *A. fallax*. Abbreviations used: GG – the Gulf of Gdansk, VM – the Vistula River mouth, * - fish scales included.

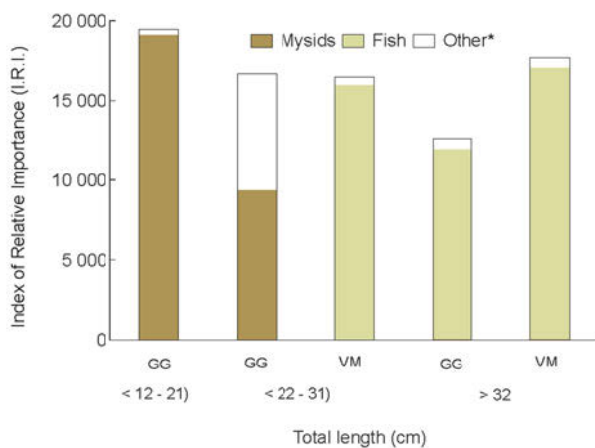


Fig. 5. Relationships between *A. fallax* length, type of habitat, and fish diet. Abbreviations used: GG – the Gulf of Gdansk, VM – the Vistula River mouth, * - fish scales included.

from the length-class of 12 to 21 cm. *O. eperlanus* was only observed in the diet of large shads (longer than 32 cm, $n=4$) from the mouth of the Vistula River, and its I.R.I. equaled 881. There were no relationships between the I.R.I. of other food items and *A. fallax* length (Table 2, Fig. 5).

DISCUSSION

In spite of obtaining stomachs from 247 specimens, only 205 organs were the subject of further analysis. In many cases the stomachs were empty. Medium shads (22 – 31 cm) (87.7%) caught

from the inshore area of the Gulf of Gdansk and large shads (longer than 32 cm) (74.0%) caught by gill nets in the Vistula River mouth both had high numbers of fish with empty stomachs. On the other hand, twaite shads from the length-class group from 12 to 21 cm caught by fishing vessels had stomachs that were more full. Specimens with III and IV degrees of stomach fullness (82.0%) were most common there.

The high incidence of empty stomachs observed in spring from the region of the Vistula River mouth may be the result of adult twaite shads ceasing to eat during the spawning migrations upriver, as described in the literature (Svetovidov 1952; Wheeler 1969; Claridge, Gardner 1978; Aprahamian 1989; Doherty, McCarthy 2002; Maitland, Hatton-Ellis 2003). During pre-spawning aggregation in shallow waters in the region of the Curonian Lagoon (Bacevičius 2007b) and when entering estuaries to spawn (Aprahamian 1981; Bracken, Kennedy 1967) the fish have only the remains of food in their stomachs. Based on the literature, Aprahamian (1989) pointed out advantages associated with reduction in feeding activity during spawning migration, such as (i) it maintains internal osmotic pressure, which allows for a greater volume for occupation by gonad material (in females this means an increase in egg number and/or size), (ii) lack of morphological and/or behavioral adaptation to feeding on benthic invertebrates (fish would have to rely on drift and/or plankton), (iii) the quantity of drift and/or plankton and size of the organisms are too small to support active feeding.

In contrast to the above mentioned studies, Redeke (1938) observed sporadic feeding of the first ascending twaite shad males (during the spawning migration in the Rhine River) on Copepoda (*Eurytemora*), Isopoda (*Asellus*), fish, and insects. Fish continued feeding in the Lower River Weser, as described by Schulze and Schirmer (2006).

The low occurrence of more full stomachs could have been influenced by additional factors making the process of digestion faster, such as warm water temperatures in the Vistula River mouth during the spring and summer, time from catching the fish to taking them out from the nets, and then time until freezing.

A. fallax from the first length-class group caught in the inshore area of the Gulf mainly fed on *M. mixta*. That species has never before been found in the twaite shad diet. Another mysid species, *N. integer*, was identified in fish stomachs, but in small

amounts – the relative weight amounted to 3%. It is a widespread prey of adult *A. fallax* in many brackish areas, e.g. in the Tagus Estuary (Assis et al. 1992), in the Severn Estuary (Aprahamian 1989), in the River Waser Estuary (Schulze, Schirmer 2006), and in the Curonian Lagoon (Bacevičius 2007b) (Table 3). Although the energy value of *M. mixta* (24.75 ± 2.47 J mg⁻¹ DW $\pm$ SD) is higher than *N. integer* (18.94 ± 1.06 J mg⁻¹ DW $\pm$ SD) (Szaniawska 1993), the varied amounts of *M. mixta* in the fish diet may result from different distributions of those species in the Gulf of Gdansk. *Mysis mixta* is the most abundant mysid in the open waters of the southern Baltic along the Polish coastline (Margoński, Maciejewska 1999), whereas *N. integer* is the most abundant mysid in the very shallow waters of the Gulf of Gdansk (Węslawski 1981). There is another difference in the size of both crustaceans. The former species reaches 30 mm in total length, and the latter approximately 17 mm (Żmudziński 1974). Juvenile *A. fallax* also feed on *N. integer* in the Curonian Lagoon (Bacevičius 2007b) and in the Elbe Estuary, where *Mesopodopsis slabberi* is the main mysid species eaten by 60 – 79 mm length twaite shad (Oesmann, Thiel 2001).

Mysids were observed in the food of each length-class of analyzed fish, but their role decreased in longer *A. fallax*. No *M. mixta* were found in the diet of medium and large shads caught in the Vistula River mouth, either because these mysids did not occur in that habitat at all, or because *A. fallax* prefers feeding on fish. The diet of the medium shad caught from the Vistula River mouth (preferred food items were fishes) was different from the shad caught from the inshore area of the Gulf of Gdansk (preferred food items were mysids). The share of fish (frequency of occurrence) in the diet of twaite shads from the Vistula mouth (88.9%; clearly dominated by *Sprattus sprattus*) was as high as in the diet of *A. fallax* from the River Tagus Estuary (83.15%) (Assis et al. 1992). Fishes (mainly *Engraulis encrasicolus*, *S. sprattus*) also are preferential food items for twaite shads from the Bay of Biscay (Taverny, Elie 2001). Different results were obtained for the River Severn Estuary and Cardigan Bay. In the first case the fish in the diet of post-spawning twaite shad adults amounted to 5.9% (*P. flesus*, *S. sprattus* and Gobiidae). The shads mainly fed on mysids (*N. integer*), Gammaridae (*Gammarus zaddachi*), and Decapoda (*Crangon crangon*). The mysid *Schistomysis spiritus* dominated in the diet, followed by fish (0+ clupeids), which were 13.6% of the diet in Cardigan Bay at the end of September/start of October (Aprahamian 1989).

Table 3

Fishes and crustaceans consumed by adult *Alosa fallax*.

Taxa	Fishing ground												
	TE	BB	SE	SR	WR	CB	WE	RB	SF	NS	RE	RW	LC
Pisces													
Clupeidae						X			X		X		
<i>Sprattus sprattus</i>		X	X				X					X	X
<i>Clupea harengus</i>									X			X	X
<i>Sardina pilchardus</i>	X											X	X
<i>Engraulis encrasicolus</i>	X	X											
<i>Osmerus eperlanus</i>												X	
Gobiidae			X										
<i>Pomatoschistus</i> sp.												X	X
<i>P. minutus</i>	X											X	
<i>P. microps</i>	X												
<i>Atherina boyeri</i>	X												
<i>Ammodytes tobianus</i>										X			
<i>Platichthys flesus</i>			X									X	
Copepoda									X		X		
Eurytemora											X		
Ostracoda						X			X				
Malacostraca									X				
Mysidacea													X
<i>Mysis mixta</i>													X
<i>Neomysis integer</i>	X		X									X	X
<i>Praunus neglectus</i>							X						
<i>Schistomysis spiritus</i>						X							
Euphasiacea	X												
<i>Nyctiphanes couchii</i>	X									X			
<i>Meganyctiphanes norvegica</i>										X			
Decapoda			X			X							
<i>Crangon crangon</i>	X	X	X									X	
<i>Palemon</i> sp.	X												
Brachyura	X												
Isopoda	X										X		
Gnathiidae	X												
Sphaeromatidae	X												
Idoteidae	X		X			X							
<i>Asellus</i>											X		
Cirrolanidae	X												
Limnoriidae	X												
Amphipoda	X	X											
<i>Corophium</i>										X			
Gammaridae	X					X	X						
<i>Gammarus zaddachi</i>		X											

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Despite their anatomical adaptation, twaite shad can feed on benthopelagic and benthonic organisms if they are swept along with the current (Assis et al. 1992). This might explain why *C. crangon*, *Palemon* sp., Idoteidae, and *Hediste diversicolor* were not found in the stomachs of *A. fallax*, although they were in the diet of twaite shad from the River Tagus Estuary (Assis et al. 1992). Similarly Gammaridae, Idoteidae, and Decapoda were also found in the stomachs of twaite shad from the Severn Estuary (Aprahamian 1989).

It seems rather curious that the fish species *Ammodytes tobianus* and the crustacean *Corophium*, both common in the Gulf of Gdansk, were not found in the digestive tracts of the analyzed *A. fallax*.

According to Svetovidov (1952) and Wheeler (1969), twaite shad feed on them. The former species was confirmed by Bacevičius (2007b), who found *A. tobianus* in twaite shad stomachs caught in the Lithuanian coastal zone (5 – 7 m). *Platichthys flesus* occasionally occurred in the food compounds of *A. fallax* from the upper Severn Estuary (Aprahamian 1989) but not in the Lithuanian studies (Bacevičius 2007b) and not in our research. Higher diversity of the food compounds of *A. fallax* occur in the estuaries outside the Baltic Sea (Tables 3, 4). In the North Atlantic, shad diets included such fish species as *Sardina pilchardus*, *E. encrasicolus*, and *Atherina boyeri*, and invertebrates, e.g. sepia *Sepia officinalis* (Assis et al. 1992).

Table 4

Insects, annelids, and molluscs consumed by adult *Alosa fallax*.

Taxa	Fishing ground												
	TE	BB	SE	SR	WR	CB	WE	RB	SF	NS	RE	RW	LC
Insecta	X										X		
Coleoptera	X	X											
Diptera	X							X					X
Simuliidae								X					
Chironominae					X								
Trichoptera					X			X					
Hydropsychidae								X					
Lepidoptera	X												
Ephemeroptera				X	X			X					
Plecoptera				X									
<i>Hediste (Nereis) diversicolor</i>	X												
Mollusca						X			X				
Lymnaeidae				X									
<i>Hydrobia</i> sp.												X	X
<i>Hydrobia ulvae</i>	X												
<i>Sepia officinalis</i>	X												

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Fish scales were observed in the stomachs of pre- or partially spawned *A. fallax* in the Severn River (Aprahamian 1989). They were recognised as *Alosa* scales and occurred in 5.2% of fish caught, using rod and line, in one of two sampling stations. In present studies, unidentified scales in the stomachs might be associated with the catch methods and/or the residues of the ingested fishes. More scales were counted in the stomachs of fish caught in the Gulf of Gdansk, but the fishing gear used to collect one big subsample is unknown (Tables 1, 2).

Plastics or synthetic fibers in the digestive tracts were also found in twaite shad from the Baltic Sea (the Lithuanian Coastal Zone and the Curonian

Lagoon) (Bacevičius 2007b), the River Tagus Estuary (Assis et al. 1992), the Severn Estuary (Claridge, Gardner 1978), and the Severn River (Aprahamian 1989). Previous observations in the Severn Estuary (Kartar et al. 1973) additionally demonstrate that other fish species (e.g. *Platichthys flesus*) swallowed the plastic debris, too. The ingested plastic may cause blockage and injury of the digestive tract and reduce feeding. Additionally, the absorption of polychlorinated biphenyls could have toxic effects (Hoss, Settle 1990; Derraik 2002). Results from our studies suggest that the Vistula River is the source of plastic debris in the Gulf of Gdansk. There is a higher frequency of occurrence of plastic in the stomachs of twaite shad (from the 21 – 32 cm length-class) caught in the mouth of the Vistula River than in fish from inshore areas of the Gulf of Gdansk. Absence of plastic in the stomachs of larger twaite shads could be explained by their ability to pass ingested debris through their stomachs.

CONCLUSIONS

The difference between twaite shads from length-class groups 12 to 21 cm, 22 to 31 cm, and longer than 32 cm and the influence of the type of habitats in their diet were observed. Smaller *A. fallax* from the Gulf of Gdansk mainly feed on mysids, whereas larger specimens are piscivorous. Fish caught in the vicinity of the Vistula River had no mysids in their stomachs.

With increasing fish length, increases in the number of fish was observed as well as the number of species they can feed on, from small gobies (*Pomatoschistus* sp.) to clupeids (*S. sprattus*) and smelt (*O. eperlanus*).

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