

# Feeding preferences of herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) in the southern Baltic Sea

Michele Casini, Massimiliano Cardinale,  
and Fredrik Arrhenius

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No field studies have been performed on the selectivity of herring and sprat in the southern Baltic Sea in relation to their entire range of prey. Accordingly, we tested in the field the following hypotheses: (i) sprat and herring are selective feeders and (ii) sprat and herring selectivity is size- and season- dependent. The results show that (i) smaller herring and all size classes of sprat are strictly zooplanktivorous, selecting principally *Temora longicornis* and *Bosmina maritima* during the autumn and *Pseudocalanus elongatus* in winter; (ii) larger herring are essentially nektobenthos feeders, predating on *Mysis mixta* during the autumn and amphipods and polychaetes during the winter; and (iii) herring and sprat seem to avoid *Acartia* spp. in both autumn and winter. During the autumn, herring are zooplanktivorous up to 18–20 cm, whereas in winter herring feed on nektobenthos starting from 14–15 cm. Selectivity was not an absolute process but it was related to prey relative abundance in the sea and, possibly, to prey profitability (e.g. size, conspicuousness, and reaction time).

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M. Casini, M. Cardinale, and F. Arrhenius: National Board of Fisheries, Institute of Marine Research, Box 4, 453 21 Lysekil, Sweden. Correspondence to M. Casini: tel: +46(0)523 18728; fax: +46(0)523 13977; e-mail: [michele.casini@fiskeriverket.se](mailto:michele.casini@fiskeriverket.se).

## Introduction

Herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) are the two most important commercial pelagic fish species in the Baltic Sea (Cardinale and Arrhenius, 2000). They are also the dominant zooplanktivorous species and the principal prey for several piscivores, thereby playing a significant role in the ecosystem of the Baltic Sea (Hansson and Rudstam, 1990; Rudstam *et al.*, 1992; Arrhenius and Hansson, 1993; Karlsson *et al.*, 1999). Most Baltic Sea studies on the diet of sprat and herring have described their stomach contents, whereas issues on their prey selectivity often have been omitted (Flinkman, 1999). Sandström (1980) was the first to highlight the selective nature of herring predation. In two more recent papers, Rudstam *et al.* (1992) and Arrhenius (1996) studied the selective predation of herring and sprat in the Northern Baltic, although zooplankton taxa were grouped at the family or even subclass level. Flinkman *et al.* (1992, 1998) were the first to compare stomach contents of Baltic herring

to contemporary zooplankton samples down to species or development stage level. Selectivity of herring in relation to zooplankton availability is well studied in the northern part of the Baltic (i.e. Flinkman *et al.*, 1992, 1998; Rudstam *et al.*, 1992; Arrhenius and Hansson, 1994; Viitasalo *et al.*, 2001). On the other hand, while investigations on feeding of herring and sprat exist (i.e. Szypula, 1992; Köster and Schnack, 1994; Szypula *et al.*, 1997a, b; Möllmann and Köster, 1999), herring selectivity is generally unknown in the southern Baltic Sea where the importance of prey other than zooplankton in the diet is greater due to the larger size range of herring in this area (Cardinale and Arrhenius, 2000). Moreover, there is no information on comparative selectivity of herring and sprat for the Baltic Sea in relation to the entire spectrum of available prey (i.e. zooplankton and nektobenthos). Sprat is a strict zooplanktivore while herring change its diet with fish size (Arrhenius and Hansson, 1993). Nevertheless, for the estimation of herring selection, nektobenthos resources have not been considered in earlier studies.

Sprat and herring growth rates have changed during the last two decades following similar patterns (Cardinale *et al.*, 2002). These variations in growth rates have been explained by changes in clupeid total abundance and/or changes in zooplankton abundance and composition. Therefore, information on the composition and dynamics of the Baltic foodweb is of fundamental importance to increase our knowledge on the Baltic ecosystem. In addition, this information is needed for a more precise assessment and prediction of fisheries resources.

We studied the feeding interactions and ontogenesis of herring and sprat in relation to all potential available feeding resources sampled nearly simultaneously in time and space. We tested the following hypotheses: (i) both sprat and herring are selective feeders and (ii) sprat and herring selectivity is size and season dependent.

## Material and methods

### Fish sampling

Fish samples were taken at six sites in the Bornholm Basin (Figure 1) during the hydroacoustic trawl survey in October 1999 and the Baltic International Fish Survey in March 2000 onboard the Swedish RV “Argos” (Table 1). The Bornholm Basin is considered one of the main feeding areas for both herring and sprat in the Southern Baltic. Fish were sampled by means of trawling (30-min hauls) during the daylight hours and were immediately (within 15 min

after trawl recovery) frozen. A subsample of at least 100 herring and 75 sprat individuals was randomly taken from each haul for stomach analysis. For all specimens, total fish length (to the nearest 0.5 cm) was recorded.

### Zooplankton sampling

Zooplankton samples were collected at 21 stations in October and 14 stations in March (three replicates at each occasion) in the Bornholm Basin (Figure 1 and Table 1). Clupeids in the Southern Baltic Sea feed upon zooplankton mainly at twilight (herring) and the first hours of the day (sprat) mostly, even though not exclusively, in the uppermost 50 m of the water column (Cardinale *et al.*, 2003) where food availability and light condition are possibly optimal (Orlowski, 2000; Cardinale *et al.*, 2003). Moreover, it has been recognized that zooplankton, in response to predation, perform diel vertical migrations (DVM) in shallow areas of the Baltic Sea, inhabiting the deeper water during the daytime and the upper water column at night (Hansson *et al.*, 1990). This pattern has been suggested also for deeper regions of the Baltic Sea (Kornilovs *et al.*, 2001) and demonstrated in areas out of the Baltic basin (Pagano *et al.*, 1993). Thus, although studies on zooplankton DVM are lacking in literature for the Bornholm Basin, in our study the zooplankton found at night in the uppermost 50 m of the water column was assumed to represent the food available for pelagic fish.

Zooplankton sampling took place during the night immediately after fish trawling using a vertical WP-2 net equipped with a 90- $\mu$ m mesh size net and a flowmeter (bottom depth range 67–86 m). The plankton net was towed vertically from a depth of 50 m (i.e. from below the thermocline) to the surface at a speed of 0.5 m s<sup>-1</sup>. Zooplankton samples were preserved in 4% formalin solution buffered with disodiumtetraborate (Dybern *et al.*, 1976). The samples were subsampled (six subsamples of the same volume) (Johansson *et al.*, 1993) and analysed under an inverted microscope at a magnification of 60 $\times$ . At least 100 specimens from each subsample were counted and identified at the species level. For copepods, adults and all the copepodite stages were considered while nauplii were excluded because a 90- $\mu$ m mesh size net does not sample them quantitatively (Flinkman *et al.*, 1992). Moreover, the incidence of nauplii in the stomachs was scarce during the study period.

### Nektobenthos sampling

Nektobenthos samples were collected with a 1-m diameter 500- $\mu$ m opening/closing Method Isaacs-Kidd (MIK) net at 21 stations, corresponding to the stations sampled for zooplankton. Due to limited ship time, sampling of nektobenthos was restricted to the autumn period. We assumed that nektobenthos found in the uppermost 70 m of

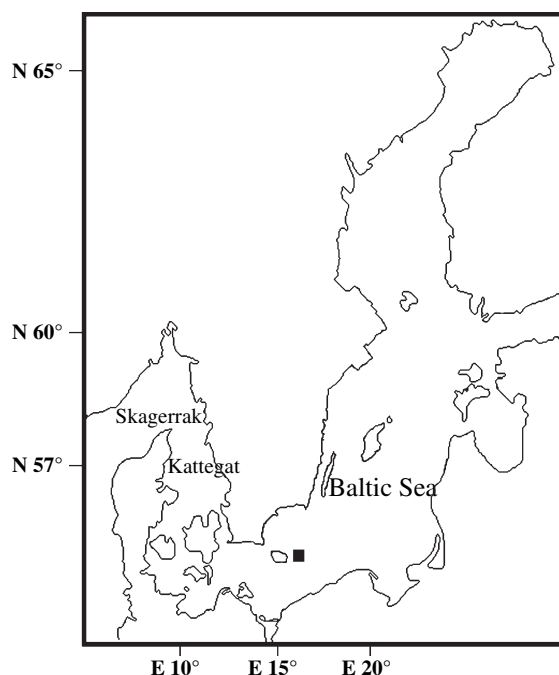


Figure 1. Map of the study area. The black quadrangle indicates the sampling location in the Bornholm Basin (see Table 1 for details).

Table 1. Summary of the sampling stations data. Samples were collected in autumn (18–20 October) 1999 and winter (8–9 March) 2000. Water temperature averaged between 0- and 50-m depth was 9.0°C and 3.3°C, in October and March, respectively. Salinity averaged between 0- and 50-m depth was 8.4 psu in October. Salinity level for March was not available.

Season	Type	Latitude (N)	Longitude (E)	Bottom depth (m)	Zooplankton wet weight (g 100 m <sup>-3</sup> )	Nekto-benthos wet weight (g 100 m <sup>-3</sup> )
Autumn 1999	WP-2 & MIK	55°27'40	15°16'00	88	5.9	1.4
	WP-2 & MIK	55°27'60	15°22'70	85	5.6	0.4
	WP-2 & MIK	55°27'60	15°29'60	85	5.5	0.4
	WP-2 & MIK	55°27'60	15°36'80	83	5.0	0.2
	WP-2 & MIK	55°27'40	15°43'50	83	5.5	0.3
	WP-2 & MIK	55°27'60	15°49'90	86	6.0	0.5
	WP-2 & MIK	55°27'50	15°56'75	84	5.5	1.0
	Pelagic trawl	55°27'85	15°37'60	78	—	—
	Pelagic trawl	55°27'40	15°20'25	86	—	—
	Pelagic trawl	55°32'60	15°16'15	77	—	—
	WP-2 & MIK	55°32'10	15°15'30	76	5.0	1.0
	WP-2 & MIK	55°32'40	15°22'20	74	5.2	0.3
	WP-2 & MIK	55°32'50	15°29'20	74	5.9	0.1
	WP-2 & MIK	55°32'40	15°36'30	74	5.7	1.2
	WP-2 & MIK	55°32'30	15°43'20	75	4.8	0.2
	WP-2 & MIK	55°32'10	15°50'20	80	5.6	0.5
	WP-2 & MIK	55°32'15	15°58'16	80	5.9	1.9
	Pelagic trawl	55°32'20	15°50'60	79	—	—
	Pelagic trawl	55°37'48	15°47'57	70	—	—
	Pelagic trawl	55°36'73	15°15'36	73	—	—
	WP-2 & MIK	55°37'50	15°13'90	73	4.7	0.6
	WP-2 & MIK	55°37'30	15°22'10	71	4.4	0.3
	WP-2 & MIK	55°37'50	15°29'70	67	4.8	1.2
	WP-2 & MIK	55°37'60	15°36'90	68	5.0	0.2
	WP-2 & MIK	55°37'60	15°44'40	68	4.0	0.1
	WP-2 & MIK	55°37'70	15°50'60	73	4.4	0.1
	WP-2 & MIK	55°37'70	15°58'40	74	4.2	0.1
Winter 2000	WP-2	55°27'40	15°16'00	88	0.5	—
	WP-2	55°27'60	15°22'70	85	0.8	—
	WP-2	55°27'60	15°29'60	85	0.8	—
	WP-2	55°27'60	15°36'80	83	0.6	—
	WP-2	55°27'40	15°43'50	83	0.7	—
	WP-2	55°27'60	15°49'90	86	1.3	—
	WP-2	55°27'50	15°56'75	84	0.6	—
	GOV trawl	55°27'85	15°37'60	81	—	—
	GOV trawl	55°27'40	15°20'25	75	—	—
	GOV trawl	55°32'60	15°16'15	76	—	—
	WP-2	55°32'10	15°15'30	76	0.8	—
	WP-2	55°32'40	15°22'20	74	0.9	—
	WP-2	55°32'50	15°29'20	74	1.1	—
	WP-2	55°32'40	15°36'30	74	0.8	—
	WP-2	55°32'30	15°43'20	75	0.9	—
	WP-2	55°32'10	15°50'20	80	0.8	—
	WP-2	55°32'15	15°58'16	80	1.2	—
	GOV trawl	55°32'20	15°50'60	76	—	—
	GOV trawl	55°37'48	15°47'57	84	—	—
	GOV trawl	55°36'73	15°15'36	79	—	—

the water column would represent the food available for pelagic fish. The MIK net was towed obliquely (45°) from a depth of 70 m (i.e. from below the thermocline) to the surface at a mean speed of 2.0 m s<sup>-1</sup>. Nekto-benthos

sampling took place during the night immediately after fish trawling (bottom depth range 67–86 m). All nekto-benthos samples were preserved in 4% formalin buffered with disodiumtetraborate (Dybern *et al.*, 1976). Nekto-benthos

individuals were identified at the species level using an inverted microscope at a magnification of 15 $\times$ .

### Fish stomach analysis

Stomach contents were collected for each individual of sprat and herring in order to determine prey abundance and composition. Zooplankton and nektobenthos, which were the two groups of food items found in the stomachs, were preserved separately in 70% alcohol. Zooplankton items were later sorted under an inverted microscope at a magnification of 60 $\times$  into taxonomic groups and identified at the species level whenever possible. A subsample of at least 100 zooplankton individuals for each stomach of herring and sprat was identified counting the carapaces (Flinkman *et al.*, 1998). Nektobenthos individuals were immediately identified at the species level using an inverted microscope at a magnification of 15 $\times$ .

The importance of the different prey types was expressed using a numerical index (NI) defined as the average proportion of individuals of the  $i_{th}$  prey type with respect to the total number of prey consumed for each fish size class (Hyslop, 1980; Linton *et al.*, 1981; Orr and Bowering, 1997).

### Statistical analysis

Data did not fulfil the assumptions of independence, homogeneous variance, normality, and linearity. Therefore, the data were log-transformed before the analysis (Sokal and Rohlf, 1995).

The mean NI of each prey item in the different seasons were tested against the different size classes (1 cm) of herring and sprat using one-way analysis of variance (ANOVA) and regression analysis (Sokal and Rohlf, 1995).

In order to determine trophic association (i.e. using the NI) among size classes of herring and sprat in the different seasons, a non-metric multi-dimensional scaling (NMDS) based on Bray–Curtis similarity was used for classification and ordination of size classes, respectively (Statistica, 1995). NMDS preserves the rank order of the inter-samples distance, as opposed to the linear relationship of classical metric scaling (i.e. Principal Component Analysis, Correspondence Analysis). NMDS has the advantage of robustness, e.g. not being sensitive to outliers and to normality and homoscedascity assumptions of classical metric scaling (Clark *et al.*, 1996). As in factor analysis, the actual orientation of axes in the final solution is arbitrary. Thus, the final orientation of axes in the plane or space is mostly the result of a subjective decision taken by the researcher, who will choose an orientation that can be most easily explained (Statistica, 1995). NMDS uses a function minimization algorithm that evaluates different configurations with the goal of maximizing the goodness-of-fit. The most common measure of goodness-of-fit used to evaluate how well (or poorly) a particular configuration reproduces the

observed distance matrix is the stress measure. Thus, the smaller the stress value, the better is the fit of the reproduced distance matrix to the observed distance matrix (Johnson and Wichern, 1998).

Selectivity was studied for each size class of herring and sprat in the different seasons using the V-index (Pearre, 1982; Flinkman *et al.*, 1992, 1998), which is based on the chi-square:

$$V = \pm (\chi^2/n)^{1/2}$$

where  $n$  is the number of observations (total abundance of zooplankton and nektobenthos in the sea and in the stomachs). The average proportion by number for each prey item of herring and sprat in the stomach and in the zooplankton and nektobenthos samples was used in the V calculation (for details see Pearre, 1982). The number of zooplankton and nektobenthos individuals per haul was standardized to 100 m<sup>3</sup> water volume. As stated above, data of nektobenthos abundance and composition were not available for the winter period and the selectivity index could not be calculated.

The V-index value ranges between 1 (absolute selection) and –1 (absolute rejection) and corresponds to zero for no selection. We used Fisher's exact test for significant difference (Sokal and Rohlf, 1995) to test for significance of selection indices as recommended by Pearre (1982).

Statistical analysis was performed using Statistica (1995) and S-Plus (2000) computer software. The level of significance was set at 5% for all the statistical tests.

## Results

### Autumn samples

The stomachs from 707 herring and 334 sprat were analysed (Table 2). The percentage of empty stomachs increased significantly with the length of fish for both herring ( $r^2 = 0.94$ ;  $p < 0.0001$ ;  $n = 16$ ) and sprat ( $r^2 = 0.74$ ;  $p < 0.003$ ;  $n = 9$ ).

Zooplankton biomass in the sea ranged between 4–6 g 100 m<sup>-3</sup> wet weight (Table 1). *Temora longicornis*, *Acartia* spp., *Evadne nordmanni*, and *Bosmina maritima* were the most abundant species in the zooplankton samples (Figure 2). *Limnocalanus grimaldi*, *Pseudocalanus elongatus* and nektobenthos species were nearly absent. Nektobenthos biomass varied from 0.1 to 1.9 g 100 m<sup>-3</sup> wet weight (Table 1).

There were marked differences in the abundance percentages of zooplankton and nektobenthos species between the sea and the stomachs of herring and sprat (Figure 2). *Acartia* spp. was frequent in the sea but not in the stomachs. Herring stomachs contained a larger abundance percentage of *T. longicornis*, while the cladocerans *Podon intermedius*, *Podon polyphemoides*, and *B. maritima* were more abundant in sprat stomachs. *Mysis mixta* and amphipods were only found in herring stomachs.

Table 2. Number of individuals and proportion of empty stomachs for each size class of herring and sprat sampled during the autumn and winter surveys.

Size class (cm)	Autumn				Winter			
	Herring	% Empty	Sprat	% Empty	Herring	% Empty	Sprat	% Empty
6			5	0				
7			7	0			5	40
8			23	0			44	45
9			8	0			136	71
10			6	17			117	68
11	3	0	57	5	6	30	207	64
12	30	0	167	12	4	25	133	56
13	62	2	53	17	8	40	44	61
14	14	0	8	25	9	33	5	100
15	44	7			24	58		
16	97	12			63	76		
17	117	21			162	83		
18	97	31			156	80		
19	73	40			152	79		
20	61	51			71	69		
21	57	53			39	85		
22	19	58			24	71		
23	13	61			10	60		
24	10	70			3	33		
25	8	63			2	100		
26	2	100			1	100		

In herring, there was a general decrease in zooplankton with increasing fish size and a significant ( $r^2 = 0.79$ ;  $p < 0.001$ ) increase of *M. mixta* (Figure 3). *T. longicornis* and *B. maritima* decreased significantly ( $r^2 = -0.53$ ;  $p < 0.003$  and  $r^2 = -0.76$ ;  $p < 0.001$ , respectively) with increasing size of herring. On the other hand, all size classes of sprat contained a high abundance percentage of *T. longicornis*, whereas the percentage of *B. maritima* increased significantly ( $r^2 = 0.71$ ;  $p < 0.005$ ) with the size of sprat.

Trophic interactions between size classes of sprat and herring were investigated by NMDS (Figure 4). Smaller herring ( $\leq 20$  cm) and larger sprat ( $\geq 11$  cm) constituted a separate group in the NMDS while large herring ( $\geq 21$  cm) and small sprat ( $\leq 10$  cm) were distinct in the ordination. A certain degree of separation was also shown for intermediate size herring (18–20 cm), which constituted a fairly distinct trophic aggregation in the NMDS compared to smaller herring.

All size classes of both herring and sprat showed a negative selection (Fisher's exact test,  $p < 0.05$ ) for *Acartia* spp. (Figure 5). Smaller herring individuals ( $\leq 20$  cm) significantly selected both *T. longicornis* and *B. maritima* while larger herring ( $\geq 18$  cm) selected *M. mixta*. Concerning sprat, most size classes selected *B. maritima*, *P. polyphemoides*, and *T. longicornis* whereas smaller individuals ( $\leq 7$  cm) fed mostly on the latter species. Figure 5 shows only the species whose V-index

was significant (either positive or negative) as calculated by Fisher's exact test (not shown).

### Winter samples

A total of 734 herring and 691 sprat were used for stomach analysis (Table 2). As for the autumn samples, the percentage of empty stomachs increased significantly with the length of both herring ( $r^2 = 0.51$ ;  $p < 0.002$ ;  $n = 16$ ) and sprat ( $r^2 = 0.51$ ;  $p < 0.05$ ;  $n = 8$ ).

Zooplankton abundance in the sea varied from 0.5 to 1.3 g 100 m<sup>-3</sup> wet weight (Table 1). *Acartia* spp., *Pseudocalanus elongatus*, *T. longicornis* and *Centrophages hamatus* were the most abundant species in the zooplankton samples, whereas *L. grimaldi* and cladoceran species were nearly absent (Figure 2).

There were noticeable differences in the abundance percentage of zooplankton species in the sea and in herring and sprat stomachs (Figure 2). *Acartia* spp. was abundant in the environment but scarce in herring and sprat stomachs. *P. elongatus* was more frequent in sprat stomachs while nekto-benthos (amphipods, *M. mixta*, and polychaetes) was found exclusively in herring stomachs.

The abundance percentage of *P. elongatus* and *T. longicornis* decreased significantly ( $r^2 = -0.61$ ;  $p < 0.001$ ;  $n = 14$ ) while polychaetes showed a significant increase ( $r^2 = 0.64$ ;  $p < 0.001$ ;  $n = 14$ ) with increasing size of herring (Figure 6). On the other hand, amphipods



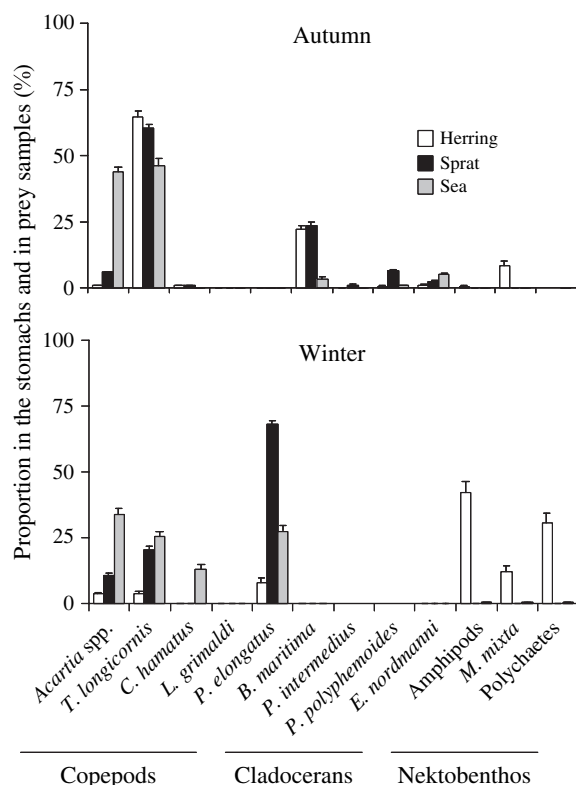


Figure 2. Proportion (by number of individuals) of prey species in herring and sprat stomachs and in the sea during the autumn and the winter. Bars represent standard errors.

and *M. mixta* were present in almost all size classes of herring and without any specific trend. Concerning sprat, the abundance percentage of *P. elongatus* decreased significantly ( $r^2 = 0.56$ ;  $p < 0.05$ ;  $n = 7$ ) with fish size, whereas *T. longicornis* showed a significant ( $r^2 = 0.68$ ;  $p < 0.05$ ;  $n = 7$ ) increase with sprat length.

NMDS (Figure 7) showed the presence of three clearly distinct trophic groups: all sprat size classes and herring small individuals (11–13 cm), medium size herring (14–22 cm), and large herring (23–24 cm).

All size classes of herring and sprat significantly avoided (Fisher's exact test,  $p < 0.05$ ) *Acartia* spp. and *C. hamatus* (Figure 8). Smaller herring (<14 cm) significantly selected *P. elongatus*, while larger individuals ( $\geq 14$  cm) avoided *P. elongatus* and *T. longicornis*. Concerning sprat, all the size classes showed a significant selection for *P. elongatus*. Figure 8 shows only the species whose V-index was significant (either positive or negative) as calculated by Fisher's exact test (not shown).

## Discussion

This study is the first attempt to estimate in the field the selectivity of herring and sprat in relation to both

zooplankton and nekto-benthos availability. Here we show that (i) small herring (<13–15 cm) and sprat are strictly zooplanktivorous, principally selecting *Temora longicornis* and *Bosmina maritima* during the autumn and *Pseudocalanus elongatus* in winter; (ii) larger herring (>15–20 cm) are essentially nekto-benthos feeders, predating *Mysis mixta* during the autumn and amphipods and polychaetes during the winter; and (iii) herring and sprat do not select *Acartia* spp. either in autumn or in winter.

Herring and sprat in the Baltic Sea form huge schools constituting around 97% of the pelagic biomass (Orlowski, 2001), performing extensive vertical migration (DVM) during the 24-hours (Orlowski, 1998, 2000, 2001; Cardinale et al., 2003) and feeding on zooplankton aggregations and, regarding herring, nekto-benthos (Arrhenius and Hansson, 1993). This implies that herring and sprat are, at least partly, potential competitors for the same available resources. However, unequivocally demonstrating competition is not a simple task, requiring information about limitation of available food resources. Nevertheless, there is evidence that zooplankton resources are a limiting factor on the growth rates of pelagic fish in the Baltic Sea (Cardinale and Arrhenius, 2000; Cardinale et al., 2002), indicating a potential intra- and inter-specific competition among pelagic fish.

Results from this study support the hypothesis (i) of highly selective feeding of both herring and sprat and (ii) that herring and sprat prey spectra are size-dependent. The favoured zooplankton prey species for sprat and smaller herring were large and conspicuous copepods such as *T. longicornis* (autumn) and *P. elongatus* (winter) and low escape response (Flinkman et al., 1998; Viitasalo et al., 2001) cladocerans such as *B. maritima* for both species and *P. polyphemoides* for sprat (autumn). These results possibly furnish indirect evidence that prey selection of herring is based on prey size, conspicuousness, and reaction time (i.e. alertness to hydrodynamic signals), as predicted by Flinkman et al. (1998) and Viitasalo et al. (2001) for herring in the Northern Baltic. Nevertheless, the same is applicable to sprat, since selectivity was similar for the two species when comparing individuals of similar size. Interestingly, herring from the Northern Baltic negatively selected *P. elongatus* in the summer (Viitasalo et al., 2001) while *P. elongatus* was positively selected in the Southern Baltic (this study) during the winter. This could be explained by the fact that in our study *P. elongatus* was, together with *Acartia* spp., the most abundant species in the sea during the winter, while the abundance of the favourite species *T. longicornis* (Viitasalo et al., 2001; this study) was particularly low compared to the autumn. Moreover, in winter, cladocerans disappeared from the zooplankton. In these circumstances, we suggest that herring and sprat fed on *P. elongatus* plausibly because it was the most abundant prey with the relatively higher profitability. These results suggest that selectivity is not an absolute process but that it depends on both the profitability of the prey (i.e. size, conspicuousness,

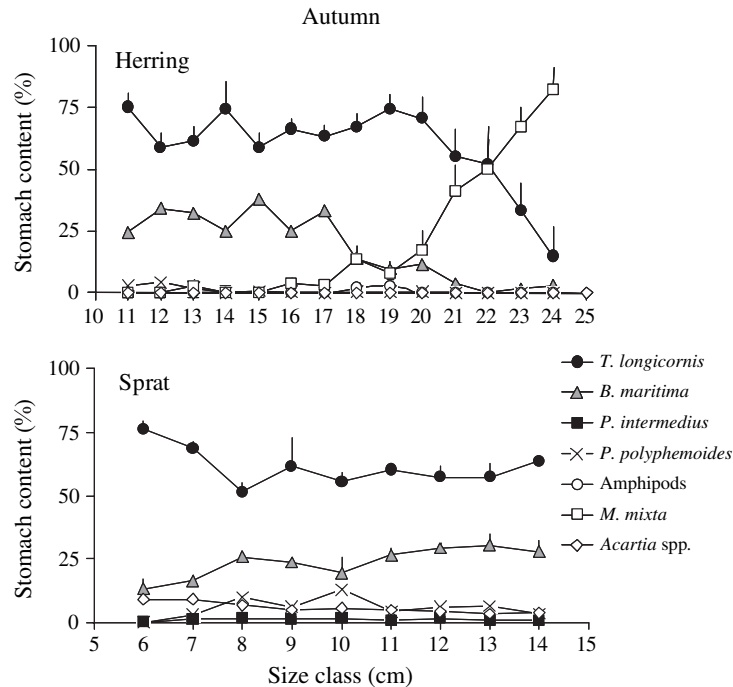


Figure 3. Proportion (by number of individuals) of prey species by size class of herring and sprat during autumn. Vertical bars represent standard errors.

and reaction time) (Viitasalo *et al.*, 2001) and the prey relative abundance (our study).

It must be held in mind that, whereas *T. longicornis*, *Acartia* spp., *C. hamatus*, and cladocera inhabit the 0–50-m depth range (Möllmann and Köster, 2002), in the Baltic deep basins the older copepodite stages (CVI) of *P. elongatus* may be distributed, especially in autumn, deeper in the water column (Möllmann and Köster, 2002). Thus, in our study, this part of the *P. elongatus* population

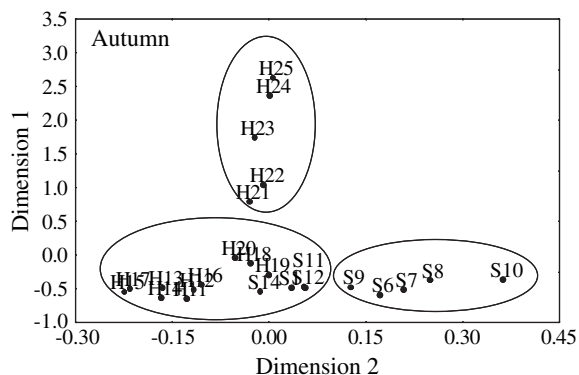


Figure 4. NMDS of the different size classes of herring and sprat stomachs sampled in autumn. The ellipses are drawn by eye and represent a subjective attempt to assemble the trophic groups found by the NMDS.

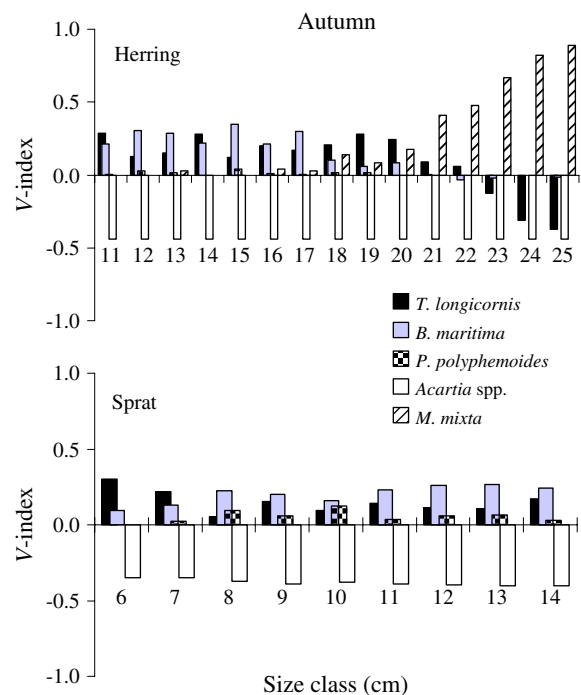


Figure 5. Selectivity (V-index) by size class of herring and sprat during the autumn. Only the species with significant V-index values, as estimated by Fisher's exact test, are shown.

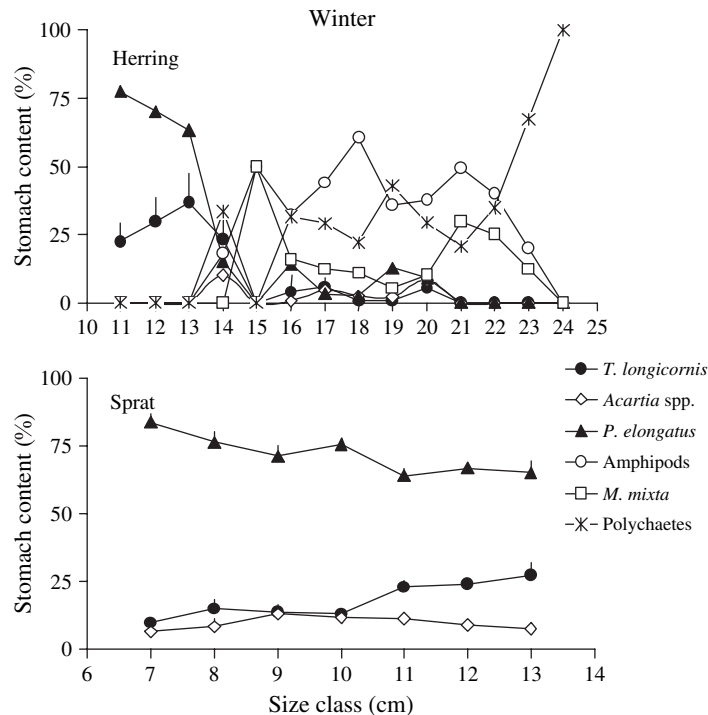


Figure 6. Proportion (by number of individuals) of prey species by size class of herring and sprat during winter. Vertical bars represent standard errors.

could not have been included in the zooplankton sampling, that covered the uppermost 50 m only of the water column, and its total abundance might have been underestimated with a consequent overestimation of the V-index. Nevertheless, since in our study the V-index was negative in autumn for both herring and sprat, we consider this result not biased. Moreover, in the study by Möllmann and Köster (2002), zooplankton samples were collected during the

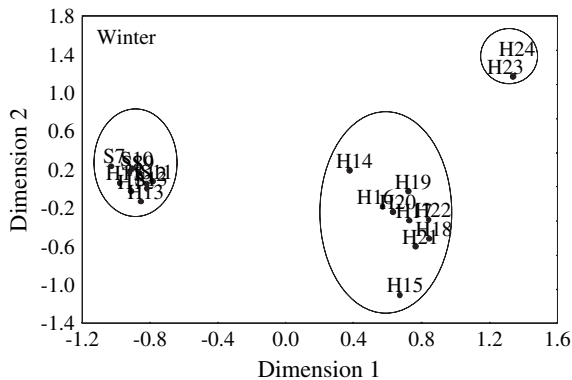


Figure 7. NMDS of the different size classes of herring and sprat stomachs sampled in winter. The ellipses are drawn by eye and represent a subjective attempt to assemble the trophic groups found by the NMDS.

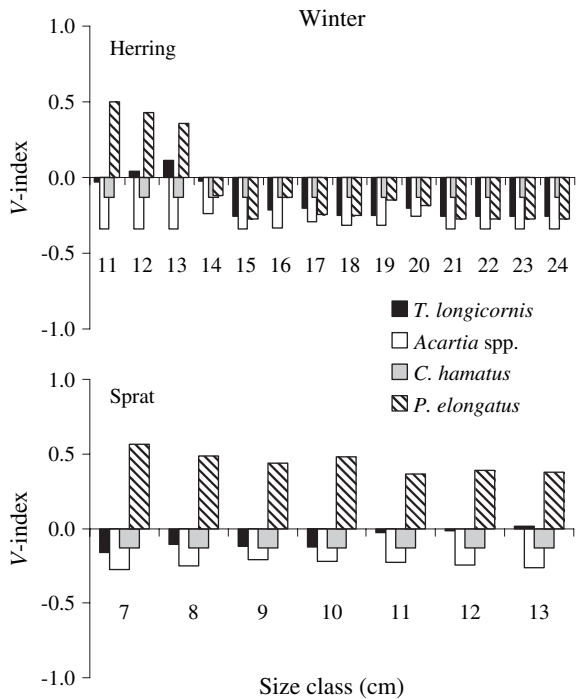


Figure 8. Selectivity (V-index) by size class of herring and sprat during the winter. Only the species with significant V-index values, as estimated by Fisher's exact test, are shown.



daytime when there is strong evidence that zooplankton inhabits deeper strata of the water column (Hansson *et al.*, 1990; Pagano *et al.*, 1993; Kornilovs *et al.*, 2001). Since in autumn in the Bornholm Basin, clupeids (especially sprat and smaller herring) feed mostly, even though not exclusively, between 0 and 50 m (Orlowski, 2000; Cardinale *et al.*, 2003), the prey found in this depth interval could reliably represent their available prey. However, we are aware that limiting the zooplankton sampling to the uppermost 50-m depth could have introduced bias in our analysis on the feeding preferences of the larger, deeper dwelling, herring.

*Acartia* spp. seemed to be always deselected even in spite of its high abundance in the sea. This result is in agreement with Möllmann and Köster (2002) who found that *Acartia* spp., despite its large abundance, was not consumed by herring and sprat in the central Baltic Sea. This could be explained by the small size and high escape response of *Acartia* spp. (Viitasalo *et al.*, 2001), but also by the fact that this genus is a surface dweller (Hansson *et al.*, 1990; Möllmann and Köster, 2002) that performs less pronounced DVM. During the daytime (when the fish samples were collected), the clupeids are distributed and may continue feeding, deeper in the water column (Köster and Schnack, 1994; Cardinale *et al.*, 2003) thus perhaps not always spatially overlapping with *Acartia* spp. during their DVM.

Another interesting result of our study is that the size of herring individuals predating on nekto-benthos changed substantially with season. During the autumn, herring was zooplanktivorous until 18–20-cm long, whereas in the winter it predated on nekto-benthos starting from 14–15-cm long. Therefore, in autumn there was a wider feeding overlap between herring and sprat, with small (11–14 cm) as well as medium size herring (15–20 cm) occupying the same trophic group as sprat. Generally, a change in diet occurs when fish approach a critical size (i.e. Ross, 1978; Cardinale, 2000). Such a scenario has been explained as means to optimize the energy intake and the time in obtaining and digesting prey as well as to avoid intra- and interspecific competition (i.e. Ross, 1978; Harmelin-Vivien *et al.*, 1989; Cardinale *et al.*, 1997). However, results from our study indicated that diet shifts are not only size (ontogenesis)-dependent but also dependent on the season and, therefore, on prey abundance and composition.

In our study we did not discriminate between zooplankton sexes and among the different copepodite stages of the copepods. Since, as showed by Viitasalo *et al.* (2001), herring can select single prey stages and sex, the results reported here must be taken cautiously and considered as representing averages on the entire stage spectrum of each prey. Additionally, we are aware that pooling 50-m depth is a wide range for fish to feed and that we were not able to resolve the feeding interactions existing between predator and prey at smaller vertical scale and to investigate the deeper strata where clupeids can continue feeding during

their DVM. As a matter of fact, interpretations, of the selection process require good information on the vertical overlap of predator and prey. Therefore, further vertical small-scale investigations, perhaps by using stratified sampling, extended to the entire water column are needed to better understand the selective feeding behaviour of clupeids in the Baltic Sea.

In the late 1980s and early 1990s, the growth rates of herring and sprat significantly decreased in all the areas of the Baltic Sea (Cardinale and Arrhenius, 2000; Cardinale *et al.*, 2002). This has been argued to occur, as a consequence of a decreased cod biomass, because of an abrupt increase in sprat abundance with a consequent density-dependent reduction in clupeid individual food intake (top–down mechanism) (Cardinale and Arrhenius, 2000; Cardinale *et al.*, 2002). On the other hand, the decrease in clupeid growth rates could also have been related, owing to unfavourable environmental condition (e.g. low-salinity levels), to a reduction in their main food items, namely *P. elongatus* and *T. longicornis* (bottom–up mechanism) (Flinkman *et al.*, 1998; Möllmann *et al.*, 2000; Cardinale *et al.*, 2002). A combination of the two mechanisms could possibly represent the most plausible explanation. Our study shows that in the southern Baltic Sea, herring and sprat utilize, at least partially, the same feeding resources by selecting/deselecting the same prey species. This could explain the positive correlation between herring and sprat growth rates observed in the Baltic Sea during the last 15 years of the past century (Cardinale *et al.*, 2002).

The concept of selective predation by consumers on specific prey types and sizes is the major process involved in top–down processes (Kitchell and Carpenter, 1993). We showed that herring and sprat select certain prey items in different periods of the year. This shows the potential for clupeids to impact the zooplankton community (Flinkman *et al.*, 1992; Kitchell and Carpenter, 1993; Möllmann and Köster, 1999, 2002). Möllmann and Köster (1999), and Rudstam *et al.* (1992, 1994) pointed out that predation by clupeids can contribute to the seasonal development of zooplankton species in the Baltic Sea. There are also indications that interannual variability of zooplankton abundance might be affected by clupeid predation pressure (Kornilovs *et al.*, 2001; Möllmann and Köster, 2002). Therefore, further studies on selectivity of planktivorous fish should be performed in order to understand better the dynamics of zooplankton/nekto-benthos populations and the mechanisms triggering the changes in clupeid growth rates.

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